FLOWER STRUCTURE AND TRENDS OF EVOLUTION IN EUDICOTS AND THEIR MAJOR SUBCLADES[1]

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Abstract

Eudicots and their currently recognized major subclades are characterized as to floral structure (including some "embryological" features) based on ca. 3000 original publications. A new classification of nucelli is presented. In particular, the distinction between tenuinucellar and incompletely tenuinucellar ovules has proven to be useful for the characterization of larger subclades. Tenuinucellar ovules characterize Gentianales, and largely Lamiales of lamiids, and Asteraceae of campanulids, thus all of the most diversified subclades of asterids. In contrast, incompletely tenuinucellar ovules are present in basal asterids and the less diversified subclades of lamiids and campanulids. Interestingly, Santalales and Caryophyllales, which have been tentatively classified in the asterid lineage s.l., have relatively thin nucelli. Also, the presence of endosperm haustoria or the particular differentiation of the embryo suspensor characterizes some larger subclades such as Fabales and Lamiales or core Saxifragales, respectively. The expanded malvids (with inclusion of Crossosomatales, Geraniales, and Myrtales) are supported by floral features. For several features that are potential key innovations, because they characterize strongly diversified clades (e.g., pentamerous flowers in core eudicots or monosymmetric flowers in Lamiales), it is shown that they are also sporadically present in species-poor clades more to the base of the phylogenetic tree. This indicates that what appear as key innovations in certain groups may be present in latent form long before their manifestation as a key innovation. Thus, it is possible that such key innovations are not always apomorphies in a strict sense (e.g., monosymmetric flowers). This conforms with results of evo-devo research, in which genetic structures connected with floral features were found in clades in which the floral features are not present.

Key words: Asterids, basal eudicots, core eudicots, eudicots, evolutionary trends, floral diversity, floral structure, ovules, perianth, rosids.

The extant angiosperms are composed of a basal grade of three small clades: *Amborella* Baill., Nymphaeales, and Austrobaileyales, and three large clades: magnoliids, monocots, and eudicots (Qiu et al., 1999; Soltis et al., 1999). Eudicots have been recognized as a clade since the structural phylogenetic studies by Donoghue and Doyle (1989) and are well supported in molecular phylogenetic analyses (Judd & Olmstead, 2004; Hilu et al., 2008; Burleigh et al., 2009; Moore et al., 2009). Eudicots are the largest clade of the angiosperms with over 200,000 species, over 300 families, and over 30 orders (Magallón et al., 1999; APG, 2009). Triaperturate pollen was recognized as a good synapomorphy for eudicots (Donoghue & Doyle, 1989) and, in particular, pollen with an aperture configuration according to Fischer's rule, i.e., apertures originating in the tetrahedral tetrad at each of the six sites where two of the four pollen grains are closest together (Doyle & Hotton, 1991). Like angiosperms as a whole, eudicots also exhibit a basal grade, and the core eudicots have two especially large clades, rosids and asterids, each of which, in turn, is associated with a basal grade. Thus, the phylogenetic tree, not only of the angiosperms as a whole but also the part of the eudicots, is highly asymmetric, reflecting unequal diversification (or unequal extinction or both) (Fig. 1).

This is a first attempt to characterize the major subclades of eudicots in their floral structures, beginning with the most inclusive clades, the supraordinal level, and going down to the level of the orders. Many of these major subclades have been newly recognized or have substantially changed in their circumscription over the past 15 to 20 years, yet have not been characterized as to their floral structure, apart from some conventional features (Bremer et al., 2001; Stevens, 2001 onward; Judd & Olmstead, 2004; Soltis et al., 2005; Judd et al., 2008; Takhtajan, 2009). The cladistic era has especially concentrated on apomorphies/synapomorphies in characterizing clades. This is certainly important. However, apomorphies are not always "characteristic" features in the sense of features of high incidence in a clade, because they may disappear again within the

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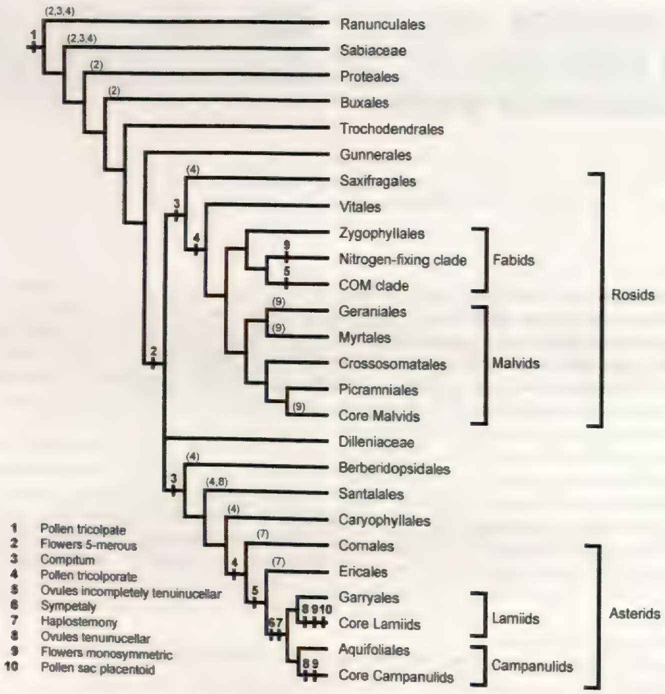

Figure 1. Cladogram of major subclades of eudicots (simplified after APG, 2009) with 10 potential key innovations (numbers in bold) and the occurrence of some of these features in other subclades where they were not key innovations (numbers in parentheses).

clade and in an extreme case may not be present in the majority of its representatives. Furthermore, apomorphies can only be determined with certainty in those parts of the phylogenetic tree that are robust, and this is still not the case for many branches. Thus, it is not always practical or feasible to characterize clades, with apomorphies, especially large clades, unless they are key innovations with a dominant representation and the branches are well supported. However, larger clades are often simply characterized by certain features that have a higher incidence than in related larger clades. Such apomorphic or homoplastic tendencies (Cantino, 1985; Sanderson, 1991) are a main topic of this study. A feature may seem to be an apomorphy of clade A within a more inclusive clade A + B, but it may have disappeared in clade B, thus technically being a plesiomorphy of clade A, or it may seem to be an apomorphy of clade A but is an apomorphy only of a large subclade of clade A or separately in more than one of its subclades. Such tendencies are quite common and deserve interest in their own right. They appear to be the result of multiple parallel evolution of particular features. From their distribution in a clade they may (ultimately) lead to hypotheses on the genetics of their evolution and the history of their establishment (see also Endress, 2005b; Shubin et al., 2009). An example of a group with a prominent tendency is the nitrogen-fixing clade consisting of the four orders Fabales, Fagales, Cucurbitales, and Rosales. All angiosperms with nitrogen-fixing bacteria in their roots are distributed in these four orders. However, only a small proportion of genera in these orders (except Fabales) exhibit this symbiosis. It has been assumed that the feature evolved independently several times in this clade because of a predisposition for the evolution of this feature (see, e.g., Soltis et al., 2005). Thus, a prediposition of a yet unknown nature for the symbiosis may be a synapomorphy in this clade, but not the presence of the symbiosis as such.

There is an immense deficit of knowledge on systematic morphology. Knowledge of the structure of plant groups at the level of alpha taxonomy, which I call here alpha morphology, is of course necessary. However, this is insufficient to understand patterns of evolution at all levels of angiosperms. A more comprehensive kind of morphology is needed based on the advances of evolutionary biology (Endress et al., 2000; Endress, 2003, 2005b, in prep.).

The present contribution on floral structure of eudicots is based on the published work of a great number of systematists and morphologists. Condensed results on rosids based on information from over 1400 original publications were published by Endress and Matthews (2006b). For the present study, ca. 1500 additional publications on core eudicots were considered, plus literature on basal eudicots (partly cited in Endress & Doyle, 2009). This literature was searched for structural features of interest for a characterization of the major subclades of eudicots.

NOTES ON CONCEPTS AND USE OF TERMS

PHYLLOTAXIS OF FLORAL ORGANS

Phyllotaxis of floral organs is defined by the divergence angles between successively initiated floral organs (e.g., Endress, 1987). It should be emphasized that the mere developmental sequence of organs is not decisive for a certain phyllotaxis pattern (which has often caused confusion in the literature). Whorled versus spiral phyllotaxis can be best distinguished by equal versus different steepness of antidromous parastichy sets and presence versus absence of orthostichies (Endress, 2006). All flowers with regularly arranged organs, regardless of whether their phyllotaxis is spiral or whorled, exhibit conspicuous patterns of spiral lines (parastichies) formed by the contiguous organs, as seen from above in young stages. These parastichies occur in several sets of certain numbers, which run in both directions (antidromous). In whorled flowers, the degree of steepness of the parastichies of two consecutive antidromous sets is equal, but in spiral flowers the degree of steepness is different. Orthostichies are straight radial lines created in the same way, but they are present exclusively in whorled flowers. Whorled patterns are either simple (with the same number of organs in all whorls, and the organs of consecutive whorls alternating) or complex (with organ number increasing or decreasing in consecutive whorls by collaterally double or multiple organ positions instead of a single organ (discussion in Staedler & Endress, 2009; see also Ronse De Craene & Smets, 1993, 1996). In irregular phyllotaxis there is no obvious pattern. It is generated in flowers with exceedingly numerous organs, especially in polymerous androecia.

Floral phyllotaxis is practically always whorled in core eudicots and also predominantly in basal eudicots, but it is spiral in some core Ranunculales, in the polymerous perianth of Nelumbonaceae and some Buxales, and sometimes in the androecium of Trochodendrales. Complex whorled patterns are present in a number of basal eudicots and some rosids but less so in asterids. Irregular phyllotaxis in the androecium occurs scattered in various groups, including Nelumbonaceae in basal eudicots, a number of rosids, and some mainly basal asterids (see also section "Merism of Floral Organ Whorls or Series" below).

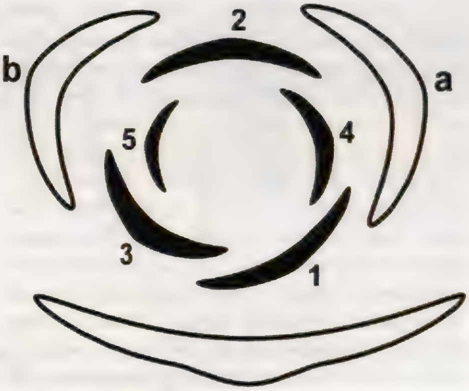

Figure 2. Diagram of outer organs in a typical 5-merous flower of eudicots. The unnumbered organ at the bottom center is the subtending bract or leaf of the flower. Organs a and b are the prophylls, which commonly have lateral positions. The black organs numbered 1 to 5 are the sepals. Prophylls and sepals form in a spiral sequence, which leads to a quincuncial aestivation of the sepals (two organs outside, one organ in between, two organs inside). The prophylls are not integrated in the floral architecture and are therefore not counted as floral organs.

MERISM OF FLORAL ORGAN WHORLS OR SERIES

Merism in flowers is defined by organ number of whorls (in whorled phyllotaxis) or series (in spiral phyllotaxis) (for a closer explanation of series, see the illustrated examples in Staedler et al., 2007). Successive whorls in a flower commonly have equal numbers of organs and their organs alternate in position (see also Ronse De Craene & Smets, 1994). Determination of merism is mostly easy because of this alternation of positions. However, in some cases it is not trivial (see section Sabiaceae). In cases with highly synorganized floral organs, alternation may be lost, probably by loss of one whorl (e.g., antepetalous stamens in subclade [III] of Ericales).

Pentamerous flowers are a prominent feature of eudicots, and contrast with the trimerous monocots. In all of the major, most species-rich clades of core eudicots, pentamery is common, both in clades with polysymmetric flowers as well as in clades with monosymmetric flowers. In basal eudicots, pentamerous flowers also occur but are not common (see notes for Ranunculales, Sabiaceae, Proteales, and Buxales).

There is a common pattern in these pentamerous flowers (Fig. 2). Flower development is commonly initiated with two lateral prophylls. It continues with the sepals (1 to 5), all in a spiral sequence. It is not a spiral phyllotaxis (Endress, 1987, 1994, 2006). Phyllotaxis is defined by the angles between subsequent organs, as explained above, and the angles of the outer floral organs correspond to those in a whorled phyllotaxis (perhaps except in the outermost two or three organs [the prophylls included]). The consequence of the spiral sequence is that sepals 1 and 2 are positioned outside, sepals 4 and 5 are inside, and sepal 3 is in between (with one margin outside and one inside). This is a characteristic disposition of sepals in core eudicots and is called "quincuncial" aestivation (Fig. 2) (Reinsch, 1926). The five young petals and the five young stamens, in contrast to the sepals, arise almost simultaneously and are in two neat whorls. Because of this, petals in eudicots are not commonly quincuncial, but often all petals have one margin outside and one inside: this is contort aestivation. Petal aestivation is often inconstant if petals are late growing, a situation that is common in many eudicots.

Although pentamery in the perianth is by far the most common pattern in core eudicots, there are also many deviations. One departure is more than five perianth organs in a whorl. In the calyx, this is often associated with a reduction in size and change of function (e.g., Asteraceae, Valerianaceae) (Semple, 2006) or loss of function (e.g., Thunbergioideae) (Schönenberger & Endress, 1998; Schönenberger, 1999; Borg et al., 2008; Endress, 2008).

Polystemony is prominent in many eudicots, especially in basal eudicots, and among core eudicots in rosids (especially malvids) and some clades of the asterid lineage s.l. (Caryophyllales, Cornales, Ericales). Stamens then develop from five primary primordia or a ring meristem. More rarely is polystemony based on a simple increase of floral or androecial radii (Apiales, Sokoloff et al., 2007a) or presence of several stamen whorls (Ranunculaceae, Schöffel, 1932; Ren et al., 2010; Rosaceae, Kania, 1973; Lindenhofer & Weber, 1999).

Multicarpelly is also quite common in various groups. But in contrast to polystemony, it is mostly based on more than five carpels in a whorl (Endress, 2002, 2006; Doyle & Endress, 2010). The presence of carpels in several whorls (or series) is rare and is, as a rule, correlated with apocarpy (in a few Ranunculales and Rosaceae).

PERIANTH

One of the ongoing problems in interpreting floral structure is the concept of sepals and petals. In contrast to stamens and carpels, which are easily defined by their specific male and female functions, such a clear distinction is not possible for sepals and petals (Endress, 2005a, 2006). The function of bud protection and optical attraction of pollinators are commonly carried out by sepals and petals, respectively. However, both functions can be fulfilled by any floral organ type and even by organs outside of the flowers, such as bracts. Conversely, both sepals and petals may also have other functions than just bud protection and optical attraction at anthesis. Specifically, petals are not always "petaloid," a term often used in the literature simply for a colored, optically conspicuous organ.

The question of homology of sepals and petals has long been addressed, recently by molecular developmental genetics and an evo-devo approach (e.g., Kramer & Irish, 2000; Irish, 2008, 2009; Di Stilio et al., 2009; Hileman & Irish, 2009; Kramer, 2009a, b; Rasmussen et al., 2009; P. S. Soltis et al., 2009) and also from a comparative point of view (Ronse De Craene, 2007, 2008), but a simple answer is not in sight.

For the time being, I use a practicable concept for eudicot perianth organs. Because most core eudicot groups have two whorls or series of perianth organs, I call the organs of the outer whorl or series sepals and those of the inner outer whorl or series petals, irrespective of their differentiation. In cases in which there are fewer or more whorls or series than two, the local phylogenetic situation is considered for an interpretation. In basal eudicots, the number of perianth organ whorls or series is often higher than two and a delimitation is sometimes more difficult. However, for problematic cases, the specific local phylogenetic neighborhood may also include cases that are easier to interpret, and from there tentative conclusions may be drawn.

OVULES

Ovules are diverse in angiosperms, but several ovular features have been shown to be stable at higher systematic levels and can be used to characterize major subclades. Of special interest are the differentiation of the nucellus at the time of the beginning of meiosis, the number and relative thickness of the integuments and their differential participation in micropyle formation, and the direction and amount of curvature of the ovules at the time of fertilization (Endress, 2003, 2005a; Endress & Matthews, 2006b). The two types of ovules, crassinucellar and tenuinucellar, which are conventionally distinguished in the embryological literature and have been widely used in systematics (e.g., Philipson, 1977), cover a relatively broad array of forms. This and the need for a finer-grained ovule classification have been repeatedly addressed (e.g., Hamann, 1977; Tobe, 1989; Shamrov,

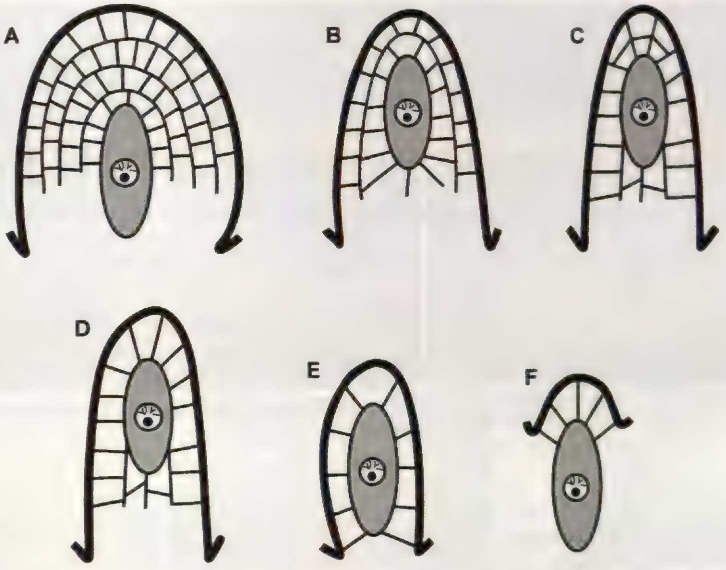

Figure 3. Classification of ovules used here (meiocyte gray). —A. Crassinucellar (with several cell layers above meiocyte). —B. Weakly crassinucellar (with two cell layers above meiocyte). —C. Pseudocrassinucellar (with one cell layer that undergoes periclinal divisions above meiocyte). —D. Incompletely tenuinucellar (with one cell layer above meiocyte and sterile tissue at its flanks and/or at the nucellus base). —E. Tenuinucellar (with one cell layer above meiocyte and no sterile tissue at its flanks or at the base of the nucellus). —F. Reduced tenuinucellar (as in E, but meiocyte longer than the nucellus, and thus with a partly "inferior" position).

1998; Endress, 2003). An extensive survey of the original literature (P.K. Endress, in prep.) shows that the diversity of forms can be compartmentalized into additional subtypes that are of interest because of their relatively stable occurrence in certain larger clades of angiosperms. These subtypes are shown in Figure 3: crassinucellar (nucellus with more than two cell layers above the meiocyte at the time of the first division) (Fig. 3A), weakly crassinucellar (nucellus with two cell layers above the meiocyte at the time of the first division, and the second cell layer not derived from the epidermis) (Fig. 3B), pseudocrassinucellar (nucellus with two cell layers above the meiocyte, the second derived from the epidermis by periclinal division; term introduced by Davis, 1964) (Fig. 3C), incompletely tenuinucellar (nucellus with only the epidermis above the meiocyte, but with sterile tissue at the flanks of the meiocyte and/or behind the meiocyte) (Fig. 3D), tenuinucellar (nucellus with only the epidermis above the meiocyte and at its flanks, and nucellus without sterile tissue behind the meiocyte) (Fig. 3E), reduced tenuinucellar (nucellus very short, with only the epidermis above the meiocyte and the meiocyte "inferior," i.e., situated partly below the nucellus) (Fig. 3F). An endothelium, a physiologically active layer of cylindrical, cytoplasm-rich cells, is commonly present in ovules with a thin nucellus, thus especially in the states depicted in Figure 3B–F. As the survey progresses, this classification may be further modified, but the present state is useful to discuss the distribution of ovule diversity in larger clades of eudicots.

Crassinucellar ovules are predominant in basal eudicots and most rosids; incompletely tenuinucellar ovules are predominant in asterids. Tenuinucellar ovules occur especially in some species-rich clades of asterids (Gentianales, Lamiales, and Asteraceae).

FLORAL NECTARIES

Nectaries are originally not independent floral organs but merely histological regions that secrete nectar and may be located on any of the floral organs. However, in derived clades they may also form more independent structures (disc nectaries) that cannot easily be relegated to one of the floral organs. In basal eudicots, nectaries are associated with stamens (some Papaveraceae and Lardizabalaceae), staminodes or petals (core Ranunculales), or carpels (Trochodendrales, Buxales). In core eudicots, disc nectaries are predominant. Similar structures also occur in some Sabiaceae and Proteaceae (collar-shaped rings around the gynoecium base). Disc nectaries are sometimes difficult to distinguish from other nectaries. I tentatively use this term for nectaries that form a ring around the gynoecium at the floral base and are elevated above the floral base in a disclike manner, thus they are of some thickness; they may be lobed between the stamen bases but characteristically form an uninterrupted ring. They are not distinctly part of the calyx, corolla, androecium, or gynoecium (see also Smets, 1986; Endress, 1994; and especially Bernardello, 2007). An exploration of the evolutionary origin of disc nectaries is beyond the scope of this paper.

MAJOR SUBCLADES OF EUDICOTS

GRADE OF BASAL EUDICOTS

The basal eudicots are a grade of three to six main clades (Hilu et al., 2003, 2008; Worberg et al., 2007; Qiu & Estabrook, 2008; APG, 2009; Burleigh et al., 2009; D. E. Soltis et al., 2009): Ranunculales, Sabiaceae, Proteales, Buxales and Trochodendrales (topology unresolved), and Gunnerales. The position of Ceratophyllales as sister to eudicots as found in a number of analyses is not sufficiently supported (see Qiu et al., in press), and they are not considered further here. The uppermost step of the grade, Gunnerales, which are sister to core eudicots, can also be treated as part of the core eudicots, as proposed by Soltis et al. (2003), because of high molecular phylogenetic support of their sister relationship. However, from a floral morphological point of view, treatment as part of the basal eudicots is more practical.

Drinnan et al. (1994) recognized that in basal eudicots there is a dominance of dimerous and trimerous whorled flowers (primarily in the perianth). In addition, Sabiaceae, with complex, somewhat puzzling monosymmetric flowers in *Meliosma* Blume, can be regarded as basically trimerous (see discussion under Sabiaceae). In three of the six orders of the basal grade of eudicots, there are genera without a perianth. Although this is only a very small fraction of the group, it is much more than in other orders of comparative size and is therefore an interesting evolutionary tendency. Perianthless flowers are present among Ranunculales in Eupteleaceae (Endress, 1969, 1986; Ren et al., 2007) and Berberidaceae (*Achlys* DC., Endress, 1989c), among Trochodendrales in Trochodendraceae (*Trochodendron* Siebold & Zucc., Endress, 1986; Wu et al., 2007), and among Buxales in Buxaceae (*Styloceras* Kunth ex A. Juss., von Balthazar & Endress, 2002a, b) and Didymelaceae (*Didymeles* Thouars, von Balthazar et al., 2003). The presence of a perianth is certainly plesiomorphic in eudicots (cf. Doyle & Endress, 2000; Endress & Doyle, 2009). The repeated loss of the entire perianth may have been possible because of only weak synorganization of floral parts (Endress, 1990). In some other genera, partly of the same families, the perianth is only weakly differentiated and bractlike: among Ranunculales in Circaeasteraceae (*Circaeaster* Maxim., Tian et al., 2005), among Trochodendrales in Trochodendraceae (*Tetracentron* Oliv., Endress, 1986; Ren et al., 2007), and among Buxales in Buxaceae (von Balthazar & Endress, 2002a, b). Concomitant with the weak differentiation of the perianth, wind pollination is relatively common, beginning with Eupteleaceae in Ranunculales, but then especially in the upper steps of the grade (Platanaceae, Buxaceae, Gunnerales). Pollen is basically tricolpate, although tricolporate in some Menispermaceae (Ranunculales), Sabiaceae, and Buxaceae (Furness et al., 2007). The gynoecium is commonly more or less apocarpous, which has been retained from the basal angiosperms (Endress & Doyle, 2009). The ovules are mostly crassinucellar and bitegmic, with the outer integument commonly thicker than the inner (Endress & Igersheim, 1999). Nectaries may be present on floral organs (petals, staminodes, stamens, or carpels), as in Ranunculales, Buxales, and Trochodendrales. In some Sabiaceae and Proteaceae, nectaries form collars around the gynoecium base. However, disc-shaped nectaries, as characteristic for many core eudicots, do not occur.

RANUNCULALES

Ranunculales comprise seven families. Eupteleaceae and Papaveraceae are successive sisters to the core Ranunculales, consisting of the five families Lardizabalaceae, Circaeasteraceae, Menispermaceae, Berberidaceae, and Ranunculaceae (Hoot & Crane, 1995; Hoot et al., 1999; Qiu et al., 2006; Worberg et al., 2007; W. Wang et al., 2009). Floral merism is most commonly two and three, but five, eight, and more also occur (Hiepko, 1965b; Endress, 1987). Spiral phyllotaxis in the perianth is less common than whorled phyllotaxis (Schöffel, 1932; Hiepko, 1965b; Ren et al., 2009, 2010). Whorled perianth phyllotaxis is primitive in Ranunculales (as in the entire eudicots) (Endress & Doyle, 2007). Elaborate monosymmetric flowers evolved in two families of Ranunculales, in Papaveraceae and in Ranunculales; in some Menispermaceae there is monosymmetry by reduction (Endress, 1999; Jabbour et al., 2009). Valvate anther dehiscence is common in Berberidaceae and rarely present in Ranunculaceae (Endress & Hufford, 1989; Endress, 1995). Nectaries, if present at all, are on the stamens, staminodes, or petals. Carpels are mostly free but fused up to the top in Papaveraceae (Endress & Igersheim, 1999). Ovules are basically crassinucellar, bitegmic, and anatropous, with a trend to incompletely tenuinucellar or pseudocrassinucellar in

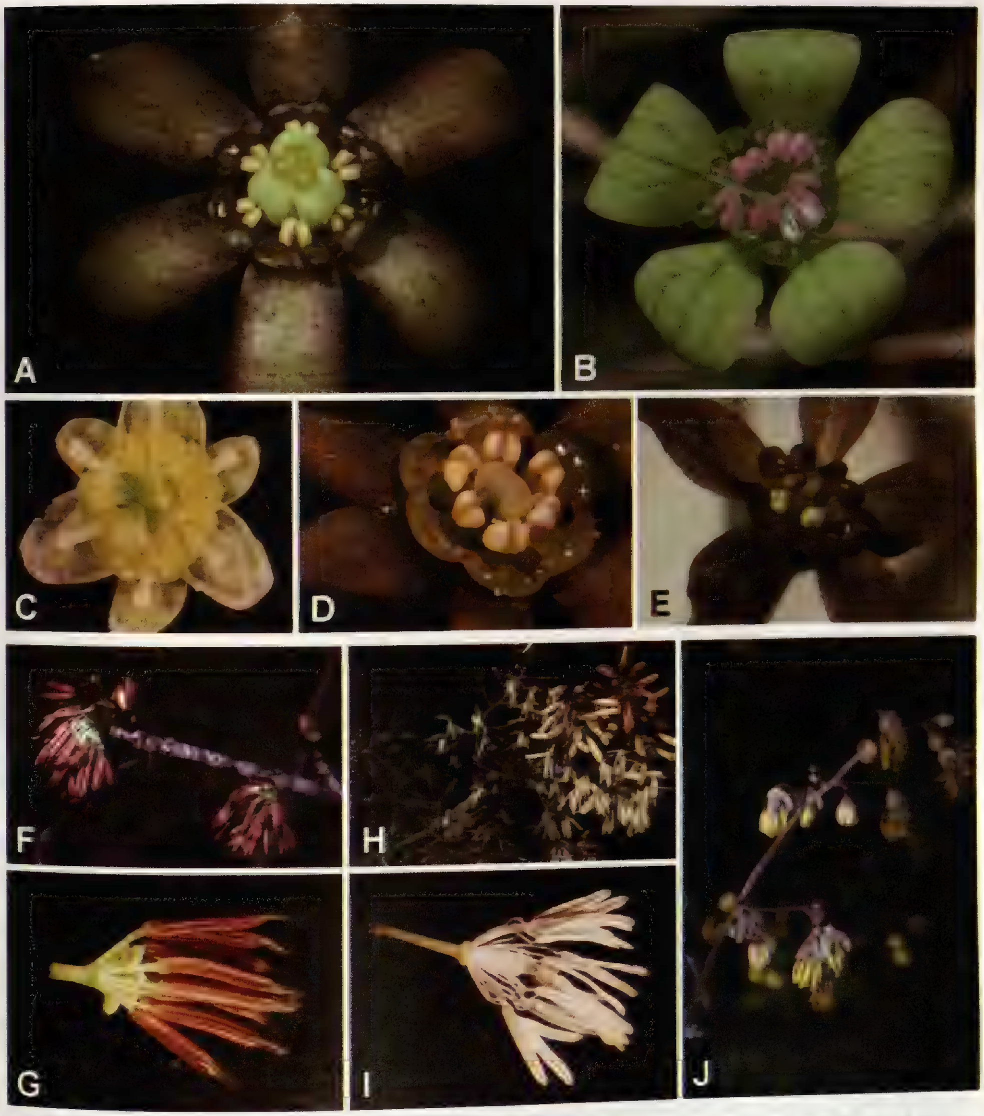

Figure 4. Ranunculales. A–E. A fly-pollination syndrome is present in at least one genus in each family of the core Ranunculales (flowers small, flat, open, dull-colored, mainly brown, green, or cream, with short, cuneate, often bilobed, nectariferous petals). —A. Lardizabalaceae (*Sinofranchetia chinensis* (Franch.) Hemsl.). —B. Circaeasteraceae (*Kingdonia uniflora* Balf. f. & W. W. Sm.) (photo by Yi Ren). —C. Menispermaceae (*Sinomenium acutum* (Thunb.) Rehder & E. H. Wilson). —D. Berberidaceae (*Caulophyllum thalictroides* (L). Michx.). —E. Ranunculaceae (*Xanthorhiza simplicissima* Marshall). F–J. A wind-pollination syndrome is present in three families of Ranunculales (flowers with caducous or lacking perianth, always without petals, and pendant stamens with long, pollen-rich anthers). —F, G. Eupteleaceae (*Euptelea polyandra* Siebold & Zucc.). —H, I. Papaveraceae (*Macleaya cordata* (Willd.) R. Br.). —J. Ranunculaceae (*Thalictrum foetidum* L.).

a few derived Papaveraceae, Circaeasteraceae, and most Ranunculaceae, to unitegmic in Ranunculaceae, Menispermaceae, and Circaeasteraceae, and to campylotropous (commonly associated with a zigzag micropyle) in some Papaveraceae, Berberidaceae, and Menispermaceae (Endress & Igersheim, 1999). The most interesting aspect of floral biology in Ranunculales is that in the core group a fly-pollination syndrome occurs in representatives of all five families: small, dull-colored, mainly greenish brown flowers with open nectar presented on the tips of staminodes (Fig. 4A–E), which are homologous to the nectariferous petals in other representatives of two of these families (Berberidaceae and Ranunculaceae) (see also Endress, 1995; Ren et al., 2004). A wind-pollination syndrome is also noteworthy because it is present in Eupteleaceae, the basalmost family of the order, and also rarely occurs in Papaveraceae and Ranunculaceae (Fig. 4F–J) (see also Endress, 2002). In these flowers, the perianth is caducous or lacking altogether, and the anthers are long and rich in pollen. The presence of wind pollination in a few Ranunculales and other orders of basal eudicots (see above) is noteworthy because it is very rare in basal angiosperms (Endress, 2010).

SABIACEAE

Sabiaceae represent the next step in the basal grade of eudicots or may form a clade with Proteales (Qiu et al., 2005). Relatively elaborate floral monosymmetry, perhaps with an explosive anther opening, is present in *Meliosma* (Ronse De Craene & Wanntorp, 2008). The flowers of *Meliosma* have been described as pentamerous with the organs positioned opposite each other, and opposite organs partly fused with each other (Stevens, 2001 onwards). However, the flowers can be easily interpreted as organized in trimerous, alternating whorls with one organ in each whorl reduced as a consequence of floral monosymmetry. In this way, the floral organization would be as in trimerous Ranunculales (e.g., Berberidaceae, Menispermaceae) or dimerous Proteaceae. In these groups, there is a tendency that stamens are basally fused with the next outer petals of the same radius. However, as the floral organs are in regular alternating trimerous whorls, these next outer petals of the same radius do not belong to the next outer floral whorl, but only to the second next outer whorl. The same is true for the dimerous whorls in Proteaceae, in which the stamens are fused (sometimes conspicuously so) with the sepals of the second next outer whorl (petals are lacking). In Berberidaceae, this synorganization between petals and stamens may be so intimate that each pair of a petal and stamen behaves as a unit. This is shown in exceptionally 5-merous terminal flowers of an inflorescence, in which five stamens remain congenitally connected with the five petals in the same radii (Endress, 1987). In this case, the alternation of organs between whorls appears no longer present. The flowers of Sabiaceae with seemingly superposed organs can be interpreted in the same way. In the floral diagram of *Meliosma* by Wanntorp and Ronse De Craene (2007), although they interpret the flowers differently, the flowers can be seen as having two transverse prophylls followed by three whorls of floral organs: (1) a whorl of three sepals, (2) a whorl of three larger petals alternating with the sepals, (3) a whorl of two small petals (one missing in the symmetry plane) alternating with the larger petals, (4) a whorl of three stamens alternating with the small petals, and (5) two stamens alternating with the outer stamens (one missing in the symmetry plane, in the radius of the missing small petal). In contrast, the flowers of *Sabia* Colebr. are polysymmetric and pentamerous (van de Water, 1980), analogous to the 5-merous terminal flowers of *Berberis* L. The two (or three) carpels are at least basally congenitally united, and in *Sabia* postgenitally united on top (van de Water, 1980; Endress & Igersheim, 1999). The two ovules per carpel are unitegmic, hemianatropous or orthotropous, and probably weakly crassinucellar in *Meliosma* and crassinucellar in *Sabia* (Mauritzon, 1936). However, more detailed research is needed. A collar-shaped nectary around the gynoecium base is present in *Sabia* (van de Water, 1980).

PROTEALES

Proteales, the third clade of basal eudicots (found by Chase et al., 1993), has three seemingly unrelated families (Fig. 5A–E). The giant flowers of Nelumbonaceae are an especially conspicuous apomorphy in a clade with otherwise much smaller flowers, comparable with the giant-flowered waterlilies among Nymphaeales, which are also primitively small flowered. Of the three families, only Proteaceae are diverse and they have a wide array of pollination adaptations, including insects, birds, mammals, and wind. However, their floral organization is uniform with consistently four sepals (with valvate aestivation), no petals, four stamens (fused with the sepals of the same radius), and one carpel, and secondary pollen presentation on the stylar head (Yeo, 1993). All Proteaceae have flowers with dimerous whorls (Douglas & Tucker, 1996, see also preceding section), modern Platanaceae have flowers with trimerous to tetramerous whorls (von Balthazar & Schönenberger, 2009), and in Nelumbonaceae flowers are polymerous, with a spiral perianth, and stamens and probably the free carpels in irregular position, the stamens arising from a primary ring primordium in centripetal sequence (Hayes et al., 2000). Interestingly, some fossil Platanaceae are pentamerous, so that the seemingly primitive trimery in modern representatives may be derived (Friis et al., 1988; Crane et al., 1993; Pedersen et al., 1994; von Balthazar & Schönenberger, 2009; Doyle & Endress, 2010), but dimerous flowers are also known from Cretaceous members (Magallón-Puebla et al., 1997). Modern Platanaceae are wind pollinated and have decurrent stigmas. Ovules are orthotropous in Platanaceae and many Proteaceae (as in Sabiaceae, see above), and the inner integument is thicker than the outer in Platanaceae and Proteaceae, but the other way around in Nelumbonaceae (Endress & Igersheim, 1999). Some Proteaceae have a collar-shaped nectary around the gynoecium base (Rao, 1971).

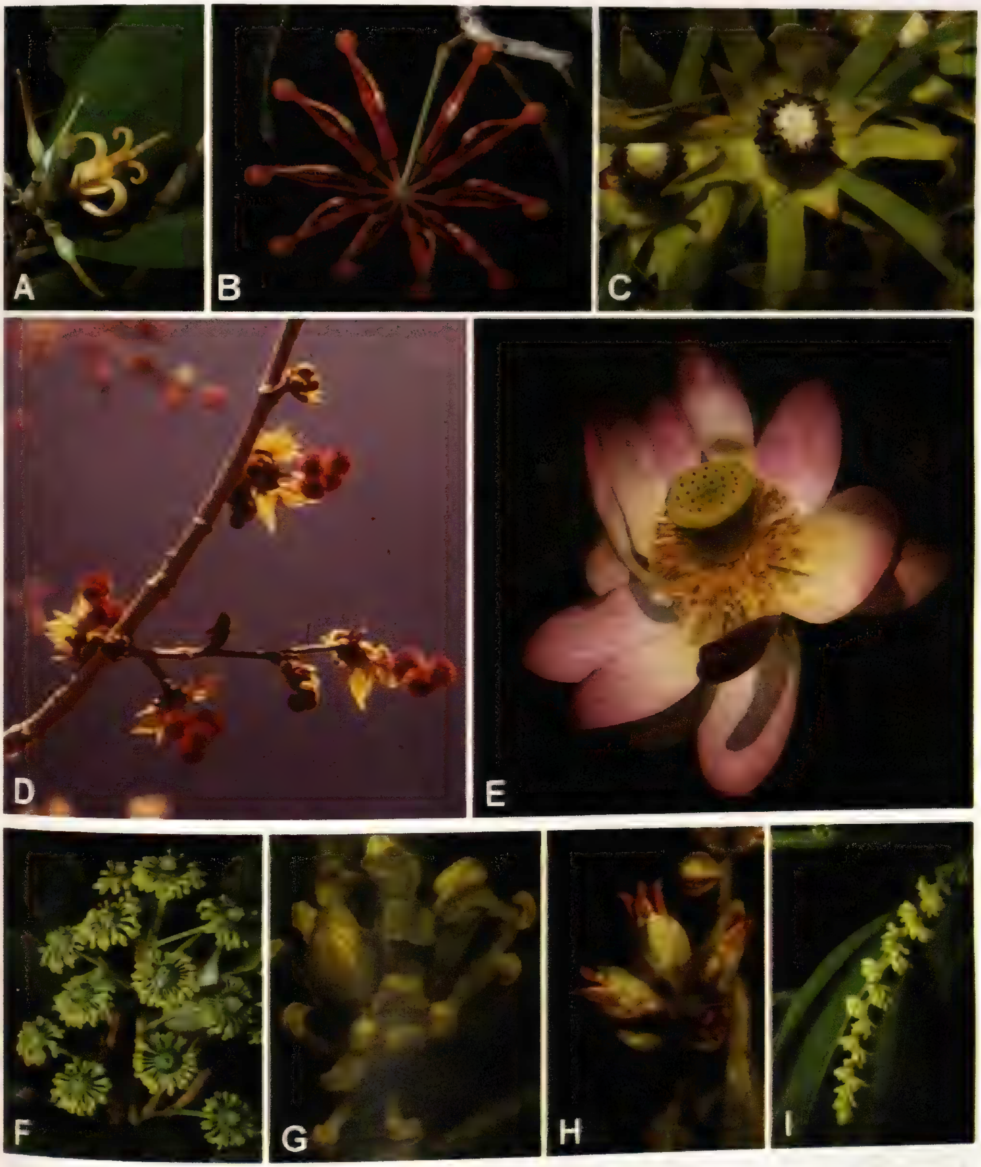

Figure 5. Proteales, Trochodendrales, and Buxales. A–E. Proteales. —A. Proteaceae (*Persoonia levis* (Cav.) Domin). —B. Proteaceae (*Stenocarpus sinuatus* (A. Cunn.) Endl.). —C. Proteaceae (*Leucadendron* R. Br. sp., male inflorescence, wind pollinated). —D. Platanaceae (*Platanus orientalis* L., male [yellow] and female [red] inflorescences, wind pollinated). —E. Nelumbonaceae (*Nelumbo nucifera* Gaertn.). —F. Trochodendrales: Trochodendraceae (*Trochodendron aralioides* Siebold & Zucc.). G–I. Buxales. —G. Buxaceae (*Buxus sempervirens* L., a female flower surrounded by male flowers). —H. Buxaceae (*Sarcococca hookeriana* Baill., male inflorescence). —I. Buxaceae (*Styloceras brokawii* A. H. Gentry & R. B. Foster, male inflorescence, wind pollinated).

TROCHODENDRALES AND BUXALES

In the next two clades, Trochodendrales (with Trochodendraceae including *Trochodendron* and *Tetracentron*) and Buxales (with Buxaceae and Didymelaceae), dimerous flowers are present in *Tetracentron* (Endress, 1986; Chen et al., 2007) and some Buxaceae (von Balthazar & Endress, 2002a, b). In both orders, polymerous flowers are also present. In Trochodendrales, *Trochodendron* is polymerous in androecium and gynoecium and shows both whorled and spiral flowers (Endress, 1990); also, its fossil relative, *Nordenskioldia*, is multicarpellate (Manchester et al., 1991; H. C. Wang et al., 2009). In Buxales, *Styloceras* and *Buxus natalensis* (Oliv.) Hutch. are polystemonous, the latter by double and multiple positions of stamens in two whorls (von Balthazar & Endress, 2002a). The perianth is simple and inconspicuous in both orders (Fig. 5F–I). Furthermore, in both orders there are genera with the perianth completely lacking: in *Trochodendron* (Endress, 1986; Wu et al., 2007), *Styloceras* (von Balthazar & Endress, 2002a, b), and *Didymeles* (Sutton, 1989; von Balthazar et al., 2003). Interestingly, in the Cretaceous (early Cenomanian) *Spanomera* Drinnan, Crane, Friis & Pedersen, the male flowers have been reconstructed as pentamerous with the five stamens superposed to the five perianth organs (Drinnan et al., 1991). The male flowers of *Spanomera* are somewhat monosymmetric and may be interpreted in the same way as those of *Meliosma* (see under Sabiales), whereas the female flowers consist of dimerous whorls (Drinnan et al., 1991). Modern Trochodendrales and Buxales have predominantly decurrent stigmas, although the presence of nectaries in at least half of the genera, always associated with the gynoecium, indicates that wind pollination does not dominate (Endress, 1986; Vogel, 1998; von Balthazar & Endress, 2002a, b). The carpels are united only at the base. The ovules are crassinucellar, bitegmic, anatropous, with the inner integument thicker than the outer (Endress & Igersheim, 1999).

GUNNERALES

Gunnerales, with Gunneraceae and Myrothamnaceae, represent the uppermost step in the basal eudicots and are sister to the core eudicots. Because this sister relationship is molecularly strongly supported, the order has been included in the core eudicots (Soltis et al., 2003). As in other basal eudicots, the flowers are mainly composed of dimerous whorls and the perianth is either lacking or inconspicuous (Jäger-Zürn, 1966; Endress, 1989e; Endress & Igersheim, 1999; Rutishauser et al., 2004; Wanntorp & Ronse De Craene, 2005; Ronse De Craene & Wanntorp, 2006; González & Bello, 2009). In both families, the flowers are at least partly unisexual, depending on their position in the inflorescence, and they have a wind-pollination syndrome. The two carpels of the (pseudomonomerous) gynoecium in Gunneraceae are united in the ovary with mostly one locule. A single crassinucellar, bitegmic, hemitropous ovule is present, with both integuments two cell layers thick (Endress & Igersheim, 1999).

CORE EUDICOTS

Core eudicots are the largest named clade in the hierarchical classification of eudicots. They are characterized by a predominance of 5-merous flowers (in contrast to the 2- and 3-merous flowers that dominate in basal eudicots). Pollen is mainly tricolporate or derived therefrom (in contrast to the simpler tricolpate forms that dominate in basal eudicots), although in basal clades of core eudicots, tricolpate pollen is still present and often coexists with tricolporate pollen in orders or families (Dilleniaceae, Saxifragales, Zygophyllales, Berberidopsidales, Santalales, Caryophyllales, Cornales, Ericales; see Erdtman, 1952). Some of the basal groups in core eudicots have spirally arranged perianth organs of an unfixed number, such as some Berberidopsidaceae (Ronse De Craene, 2004), Dilleniaceae (Endress, 1997b), and Paeoniaceae in Saxifragales (Hiepko, 1965a). Studies in the floral phyllotaxis of basal eudicots indicate that this condition is derived at this level and not primitive (Endress & Doyle, 2007), in contrast to Ronse De Craene (2004).

Rosids and asterids are two especially large and diverse groups of the core eudicots. There are several classical floral characters that roughly distinguish rosids and asterids: (1) petals free versus united, (2) stamens in two whorls and not fused with petals versus a single whorl and fused with petals, (3) ovules bitegmic, crassinucellar, and without endothelium versus unitegmic, tenuinucellar, and with endothelium, and (4) endosperm haustoria rare versus common. An additional difference, which needs more study, is presence versus absence of special mucilage cells in flowers (Matthews & Endress, 2006). A previously unreported difference is that a number of clades in asterids have completely unvascularized ovules, whereas this does not appear to be the case in rosids. This needs more comparative study. A surprising feature is a difference in behavior in those groups of rosids and asterids that have contort petal aestivation. In asterids, the direction of contortion is always fixed in a species, genus, or even family. In contrast, in most rosids both directions are present in the same individual (Endress, 1999, 2001a).

There are two common contrasting alternative strategies that repeatedly evolved in both rosids and asterids but with different distribution in the subclades: (1) small simple flowers, often functionally unisexual, the petals often with both protective and attractive functions (many rosids, some asterids; e.g., many Celastrales, Sapindales, Apiales), and (2) elaborate, complex flowers with dichogamy/

herkogamy mechanisms, often monosymmetric (some rosids, many asterids; e.g., Fabales, Lamiales, Asterales), in part with secondary pollen presentation.

DILLENIACEAE

Dilleniaceae have an unresolved position at the base of core eudicots (APG, 2009). The flowers of most genera are polystemonous and apocarpous (Horn, 2009). There are most often five petals, but three are not uncommon. These numbers and developmental observations in *Dillenia* L. (Endress, 1997b) indicate that perianth phyllotaxis may be spiral. In *Dillenia*, flower size is conspicuously increased, associated with a further increase in stamen number and an increase in carpel number and carpel fusion (Endress, 1997b; Horn, 2009). Androecial asymmetry occurs in two unrelated clades (*Schumacheria* Vahl and *Hibbertia* Andrews, p.p.; Horn, 2009). Ovules are bitegmic, pronouncedly crassinucellar, somewhat campylotropous, with a zigzag micropyle, and the inner integument thicker than the outer (Sastri, 1958). The entire family appears to have short-lived pollen flowers without nectaries and is bee pollinated (Endress, 1997b).

ROSIDS

Rosids are systematically relatively well circumscribed (H. C. Wang et al., 2009) and represent the largest subclade of core eudicots in terms of number of orders and families. However, there are still many unresolved topologies between larger subclades of rosids, which may reflect their rapid early radiation in the Cretaceous (H. C. Wang et al., 2009). A comparison of floral structures in the major subclades was attempted by Endress and Matthews (2006b), and comparison with fossils was discussed by Endress and Friis (2006) and Schönenberger and von Balthazar (2006). See also general notes on rosids under Core Eudicots.

SAXIFRAGALES

Saxifragales, the basalmost clade in rosids s.l. (not included in rosids in APG, 2009), appear to consist of three main clades: (1) Paeoniaceae plus Peridiscaceae (not strongly supported), (2) the so-called woody families (Altingiaceae, Cercidiphyllaceae, Daphniphyllaceae, Hamamelidaceae), and (3) the core Saxifragales (Aphanopetalaceae, Haloragaceae, Crassulaceae, Iteaceae, Penthoraceae, Pterostemonaceae, Saxifragaceae, Grossulariaceae) (Jian et al., 2008). The woody families have a poorly differentiated perianth or no perianth at all, and are completely or partly wind pollinated. In these families (except for a few Hamamelidaceae), floral nectaries are absent. In petaliferous families, the petals have a narrow base and are commonly retarded in bud. Another extreme are Paeoniaceae with much enlarged flowers, and mainly pollen as a reward for pollinators. Paeoniaceae and Peridiscaceae share the absence of petals (the seeming petals in Paeoniaceae are sepals, Hiepko, 1965b) and polystemony (Davis & Chase, 2004; Bayer, 2007) with centrifugal initiation in Paeoniaceae (Hiepko, 1965a). Moderate polystemony also occurs in a few Hamamelidaceae, and notably with both centripetal and centrifugal initiation patterns (Endress, 1976). If nectaries are present, they form a ring (shallow, not disclike) around the ovary base (Iteaceae, Saxifragaceae) (Bensel & Palser, 1975), or scales (disc lobes) between the stamens (some Hamamelidaceae, Endress 1989b) or at the back of the carpels (Crassulaceae) (Wassmer, 1955); in some other Hamamelidaceae, nectaries are on staminodes or petals (Endress, 1989b). Elaborate disc nectaries, as present in many eurosids, do not occur in Saxifragales. Basifixed anthers are common (in contrast to dorsifixed anthers as in many other rosids; Hufford & Endress, 1989; Endress & Stumpf, 1991; Hermsen et al., 2006). Some families have largely or completely free carpels (Altingiaceae, Cercidiphyllaceae, Paeoniaceae, Saxifragaceae, Crassulaceae). Presence of two carpels is common; however, gynoecia are isomerous with the outer floral whorls in Crassulaceae, Haloragaceae, Aphanopetalaceae, and Penthoraceae, or there are at least more than two carpels in Paeoniaceae and Peridiscaceae. Ovary position is conspicuously labile, fluctuating between inferior, semi-inferior, and superior at family level, sometimes even within a genus (Hamamelidaceae, Endress, 1967, 1989d; *Corylopsis* Siebold & Zucc., Endress, 1989d; Saxifragaceae, Morf, 1950; Soltis & Hufford, 2002; *Lithophragma* (Nutt.) Torr. & A. Gray, Kuzoff et al., 1999). The ovules are anatropous and commonly crassinucellar, but weakly crassinucellar in some Saxifragaceae, Crassulaceae, and Haloragaceae (Stolt, 1928; Mauritzon, 1933); they are bitegmic (except for a few unitegmic Saxifragaceae, Mauritzon, 1933). In the taxa of several families, the presence of more than two meiocytes in the nucellus has been recorded (Aphanopetalaceae, Mauritzon, 1939; Crassulaceae, Mauritzon, 1933; Hamamelidaceae, Endress, 1977; Paeoniaceae, Walters, 1962). Commonly, the outer integument is thicker than the inner or both are equally thick, and the micropyle is formed by both integuments. Ovules are not yet mature at anthesis in Altingiaceae, Cercidiphyllaceae, and some Hamamelidaceae, a feature associated with flowering in early spring (Endress, 1967, 1977, unpublished). Endosperm haustoria are reported from Crassulaceae (Mauritzon, 1933). More strikingly, embryo suspensor haustoria are formed by the greatly enlarged terminal cells in members of core Saxifragales (Crassulaceae and Saxifragaceae, Vignon-Fétré, 1968; Haloragaceae, Bawa, 1969). A unique feature within rosids is valvate anther dehiscence in Hamamelidaceae. The state reappeared here in isolation after it had been more common in basal eudicots (and basal angiosperms) (Endress, 1986, 1989a, b, d; Hufford & Endress, 1989; Magallón, 2007). In the unusually rich Cretaceous fossil record of the family, valvate dehiscence is well represented (Friis & Endress, 1990; Endress & Friis, 1991; Magallón-Puebla et al., 1996; Magallón et al., 2001; Magallón, 2007).

VITALES

Flowers of the only family in the order, Vitaceae, are remarkably uniform. They are tetramerous or pentamerous, haplostemonous, and have a mostly dimerous gynoecium. Sepals are united and form a short rim. Petals are induplicative valvate and postgenitally united in bud and form a massive protective cover (e.g., Gerrath & Posluszny, 1989). Stamens are antepetalous. In *Leea* D. Royen ex L., both petals and stamens are basally congenitally united and, in addition, they together form a basal tube (Nair & Nambisan, 1957). The carpels are congenitally united up to the stigma (Gerrath & Posluszny, 1989). The ovary fluctuates between superior and semi-inferior (Kashyap, 1957). The two ovules per carpel are on an axile placenta (Gerrath & Posluszny, 1989). Ovules are anatropous and pronouncedly crassinucellar, with a nucellar cap (Berlese, 1892). The outer integument is thicker than the inner, and both or only the inner form the micropyle. A well-developed nectary disc is present between androecium and gynoecium.

EUROSIDS

Eurosids contain two major groups: fabids and malvids. Fabids again contain two major subgroups: the nitrogen-fixing clade and the Celastrales–Oxalidales–Malpighiales (COM) clade. Two or three additional clades form again a basal grade. A new order, Huerteales, was recognized recently in malvids (Worberg et al., 2009) with the families Gerrardinaceae, Tapisciaceae, and Dipentodontaceae. The floral structure of its components is very poorly known, and so the order cannot yet be structurally characterized. *Tapiscia* Oliv. and *Huertea* Ruiz & Pav. were seen as a somewhat aberrant subgroup of Staphyleaceae (now in Crossosomatales) for a long time (Krause, 1942). *Perrottetia* Kunth and *Dipentodon* Dunn were previously placed in Celastraceae, but floral structure of *Perrottetia* showed it to be clearly out of place there (Matthews & Endress, 2005a), and *Gerrardina* Oliv. was placed in Flacourtiaceae (Malpighiales) before it was recognized as constituting a separate family (Alford, 2006). The position of Myrtales and Geraniales in the malvid clade is new (Burleigh et al., 2009). Furthermore, in analyses based on mitochondrial genes (Zhu et al., 2007; Qiu et al., in press), the COM clade appeared to come with the malvids instead of the fabids. Interestingly, this relationship had been tentatively suggested earlier by Endress and Matthews (2006b) based on floral structural data. It is important to emphasize that, although the different orders are relatively strongly supported by molecular systematic analyses, this is not always the case for the relationships between the orders. Therefore, details of the topology will most probably change in the future with denser taxon sampling.

FABIDS (EUROSIDS I)

In APG (2009), core fabids have two large subclades that are sister to each other, the nitrogen-fixing clade and the COM clade. Zygophyllales are sister to them. However, fabids are structurally not easily characterized, especially as the position of the COM clade is uncertain (see above), and thus the circumscription of fabids is uncertain.

ZYGOPHYLLALES

Zygophyllales contain two families, Zygophyllaceae and Krameriaceae (APG, 2009). Flowers of Zygophyllaceae are polysymmetric; those of Krameriaceae, elaborate oil flowers, are monosymmetric (Vogel, 1974). Flowers are basically pentamerous, diplostemonous or (rarely) haplostemonous, with five or three carpels (Nair & Nathawat, 1958; Narayana & Rao, 1963); however, in Krameriaceae, stamen number is reduced to two and the gynoecium is pseudomonomerous (Leinfellner, 1971; Simpson, 1982). The petals are retarded in early development (Ronse De Craene & Smets, 1995). The carpels are congenitally united up to the stigma. Ovules are weakly crassinucellar in *Balanites* Delile (Nair & Jain, 1956; Boesewinkel, 1994), *Fagonia* L. (Nair & Gupta, 1961), *Zygophyllum* L. (Masand, 1963), and Krameriaceae (Verkerke, 1985a); those of Zygophyllaceae are associated with an endothelium. The micropyle is formed by the inner integument in *Krameria* Loefl. (Verkerke, 1985a) and most Zygophyllaceae (Mauritzon, 1934; Kamelina, 1985), but a zigzag micropyle is present in *Balanites* (Boesewinkel, 1994). The outer integument is thicker than the inner in both families (Verkerke, 1985a; Boesewinkel, 1994).

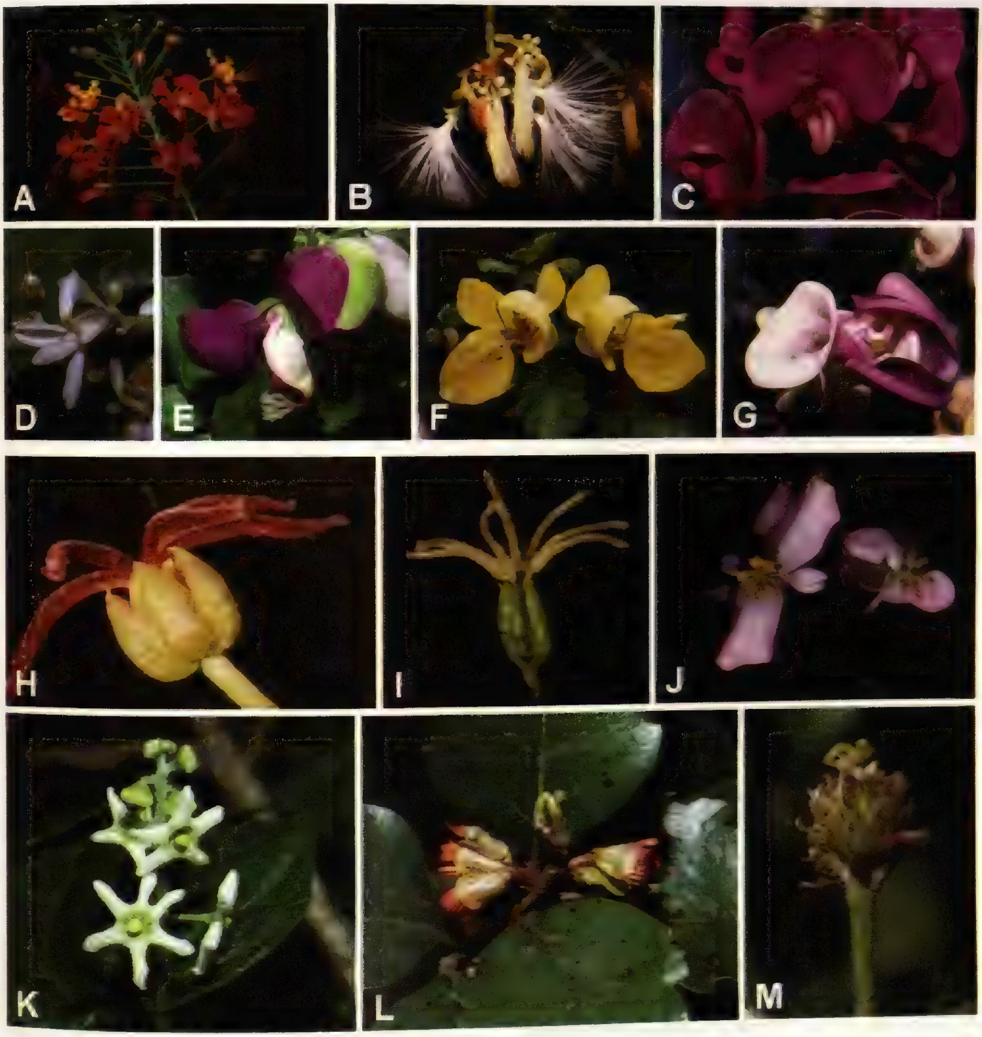

Figure 6. Fabales, Cucurbitales, and Fagales. A–G. Fabales. A–C. Fabaceae. Diversity in flower forms in major subgroups of the family. —A. Caesalpinioids (*Caesalpinia pulcherrima* (L.) Sw.). —B. Mimosoideae (*Inga feuillei* DC.). —C. Papilionoideae (*Lathyrus latifolius* L.). D, E. Polygalaceae. —D. *Xanthophyllum octandrum* (F. Muell.) Domin. —E. *Polygala myrtifolia* L. E–G. Polygalaceae and Fabaceae with conspicuously asymmetric flowers. —F. *Senna aversiflora* (Herb.) H. S. Irwin & Barneby (photo by Brigitte Marazzi). —G. *Vigna caracalla* (L.) Verdc. H–K. Cucurbitales. —H. Coriariaceae (*Coriaria myrtifolia* L., wind pollinated). —I. Datiscaceae (*Datisca cannabina* L., female flower, wind pollinated). —J. Begoniaceae (*Begonia* sp., male and female flower). —K. Cucurbitaceae (*Marah fabacea* Greene). L, M. Fagales. —L. Nothofagaceae (*Nothofagus truncata* (Colenso) Cockayne, male inflorescence, wind pollinated). —M. Fagaceae (*Fagus sylvatica* L., female inflorescence, wind pollinated).

NITROGEN-FIXING CLADE (FABALES, ROSALES, CUCURBITALES, FAGALES)

This well-supported clade is made up of all four orders in which nitrogen-fixing bacteria occur in the roots of at least some representatives. To date, it is not so easy to characterize the clade by floral structural features. In all orders there are groups with reduced, apetalous, wind-pollinated, structurally unisexual flowers with uniovulate carpels or gynoecia (least in Fabales) (Endress & Matthews, 2006b). Synsepaly is relatively common. In both larger groups with reduced flowers (Fagales and the subclade of Rosales consisting of the former Urticales), the presence of coenosomes in the inflorescences is noteworthy (i.e., cymose branching systems that form compact bodies). They are present as the cupules in Fagales (Fagaceae [Fig. 6M], Nothofagaceae, and perhaps Myricaceae)

(Macdonald, 1980; Fey & Endress, 1983; Rozefelds & Drinnan, 2002) and as the congested, sometimes flat or urceolate, inflorescences of Moraceae and Urticaceae (Rosales) (Bernbeck, 1932). Ovules are largely crassinucellar. Ovules with several meiocytes were recorded among Rosales in a number of Rosaceae and Rhamnaceae, and among Fagales in Betulaceae, Casuarinaceae, and Fagaceae. Chalazogamy (or, better, non-porogamy) associated with delayed ovule maturation is known from several Fagales (Sogo & Tobe, 2008) and from single Rosaceae and Ulmaceae (Nawaschin, 1898; Murbeck, 1901; Shattuck, 1905). Orthotropous ovules occur in Juglandaceae and Myricaceae (Fagales) and Urticaceae (Rosales). Unitegmic ovules and ovules with vascular bundles in the integument(s) are known from representatives of all four orders. In bitegmic ovules, the outer integument is usually thicker than the inner. In addition, in some taxa the inner integument is retarded compared to the outer and does not contribute to the micropyle (many Fabaceae from all major subgroups, Prakash, 1987; Polygalaceae p.p., Verkerke, 1985b; Rhamnaceae (Rosales), Arora, 1953; Begoniaceae, Datiscaceae (Cucurbitales), Matthews & Endress, 2004).

FABALES

Fabales are one of those completely new orders derived from recent molecular phylogenetic studies (Bello et al., 2009). It consists of four families (Fabaceae, Polygalaceae, Quillajaceae, Surianaceae) that have not been together in earlier classifications (the relationship of the two larger families Fabaceae and Polygalaceae was first recognized by Chase et al., 1993). Fabaceae and Polygalaceae are characterized by monosymmetric flowers, in many cases complex keel flowers with the reproductive organs hidden in the lower petals, but with different organization (Fig. 6C–G) (Endress, 1994; Westerkamp & Weber, 1999; McMahon & Hufford, 2002, 2005; Prenner, 2004a; Lewis et al., 2005; Tucker, 2006; Sokoloff et al., 2007b; Bello et al., 2010) and secondary pollen presentation at the tip of the keel. Fabaceae are one of the most species-rich and most diverse angiosperm families. In addition to keel flowers (Papilionoideae), brush flowers with long stamens and short petals (Mimosoideae) and more open flowers with expanded petals are present (caesalpinioids, not monophyletic) (Fig. 6A–C) (Polhill & Raven, 1981; Tucker, 1987, 2003; Herendeen et al., 2003). In both families of Fabales with monosymmetric flowers, Fabaceae and Polygalaceae, asymmetric flowers occur as a further elaboration (Fig. 6E–G) (Westerkamp, 1993; Westerkamp & Weber, 1999; Prenner, 2004a, b; Marazzi et al., 2006; Marazzi & Endress, 2008). Synsepaly is present in many Fabaceae and in *Stylobasium* Desf. (Surianaceae) (Carlquist, 1978). Petals have narrow bases and tend to be conspicuously delayed in early development (Polygalaceae, Prenner, 2004a; Fabaceae, Tucker, 2006; Quillajaceae and Surianaceae, Bello et al., 2007). Free carpels are common, except for Polygalaceae (Bello et al., 2007); a single carpel occurs in almost all Fabaceae and in three of the five genera of Surianaceae (Schneider, 2007). Ovules are commonly crassinucellar, bitegmic, and often anatropous, but in Surianaceae (Heo & Tobe, 1994) and many Fabaceae, they are campylotropous (Prakash, 1987). A chalazal endosperm haustorium is common in Fabaceae (Prakash, 1987) and also occurs in some Polygalaceae (Rao & Roy, 1981) and Surianaceae (Heo & Tobe, 1994). Zigzag micropyles are present in many Fabaceae (Prakash, 1987) and Polygalaceae (Verkerke, 1985b). Seeds with arils occur in a number of Fabaceae and Polygalaceae.

ROSALES

The major phylogenetic split in Rosales is between Rosaceae and the remaining group of families, which consist of two major subclades: the former Urticales (currently four families) and a clade of Barbeyaceae, Dirachmaceae, Elaeagnaceae, and the perhaps polyphyletic Rhamnaceae (Sytsma et al., 2002). Petals, if present, have a narrow base. However, there are relatively many Rosales that lack petals, such as all families of the former Urticales, Barbeyaceae, Elaeagnaceae, and some Rhamnaceae and Rosaceae; many of these have completely unisexual flowers and are wind pollinated. Haplostemony is predominant (all families of the former Urticales, Barbeyaceae, Dirachmaceae, Rhamnaceae, most Elaeagnaceae, and some Rosaceae). However, in Rosaceae, polystemony including several stamen whorls and beginning with a complex whorl by double stamen positions is predominant (Murbeck, 1941; Kania, 1973; Lindenhofer & Weber, 1999). Presence of a single crassinucellar, anatropous ovule per carpel or per gynoecium is common (former Urticales, Shattuck, 1905; Fagerlind, 1944; S. P. Singh, 1954; Barbeyaceae, Dirachmaceae, and Elaeagnaceae, Ronse De Craene & Miller, 2004; Rhamnaceae, Prichard, 1955; Rosaceae, Juel, 1918). The largest family, Rosaceae, has a considerable diversity of floral forms, with or without petals, with a varying number of stamen whorls, with carpel number ranging from one to several hundred (and then in several whorls), carpels free or united in the ovary, and ovary varying from superior to inferior.

CUCURBITALES AND FAGALES

In Cucurbitales and Fagales there is a trend toward trimerous and dimerous flowers in some families that is sometimes associated with the absence of petals, completely unisexual flowers, and wind pollination (Fig. 6H–M). Trimerous and dimerous flowers occur in Nothofagaceae, Fagaceae, and Betulaceae among Fagales, and in Datiscaceae, Begoniaceae, and Cucurbitaceae among Cucurbitales. Petals are absent in all Fagales and, among Cucurbitales, in Datiscaceae, Begoniaceae, and some Anisophylleaceae and Cucurbitaceae (Matthews et al., 2001; Matthews & Endress, 2004). If petals are present, they are always pointed (Matthews & Endress, 2004). Unisexual flowers uniformly occur in all Fagales and consistently or partly in each family of Cucurbitales (Matthews & Endress, 2004; Garnock-Jones et al., 2007). However, Cretaceous Fagales and Cucurbitales may have had bisexual flowers (Friis et al., 2006b) and thus unisexual flowers may not be a synapomorphy for this subclade, and wind pollination may have evolved separately several times (Manos et al., 2001; Oh & Manos, 2008). Inferior ovaries are predominant in both orders. In addition, sometimes the flowers have a neck, a long intercalated zone between the base of the outer floral organs and the inferior ovary (Cucurbitaceae, Fagaceae). A tendency to form long, unifacial stigmatic branches occurs in both orders (several families in Cucurbitales, Matthews & Endress, 2004; Betulaceae, Endress, 1967). In addition, stigmatic lobes are bifurcate in several families of Cucurbitales and in some Juglandaceae of Fagales (Manning, 1940; Matthews & Endress, 2004). In the ovules, there is a trend to unitegmy (most Fagales, partly in Coriariaceae and Anisophylleaceae of Cucurbitales) (Matthews & Endress, 2004). Fagales have a rich Cretaceous floral fossil record indicating a high diversification of flowers at that time (Herendeen et al., 1995; Sims et al., 1999; Schönenberger et al., 2001; Friis et al., 2003, 2006a, b; Takahashi et al., 2008).

COM CLADE (CELASTRALES, OXALIDALES, AND MALPIGHIALES)

The COM clade (informal name introduced by Endress & Matthews, 2006b) is a well-supported clade of three orders, Celastrales, Oxalidales, and Malpighiales (Soltis et al., 2000; Wurdack & Davis, 2009). There is a tendency to form fringed or lobed petals or staminodes (Endress & Matthews, 2006a). In all three orders, there are some instances with the petals postgenitally united at the base (in some by marginal hooks) (Celastraceae, Matthews & Endress, 2005a; Oxalidaceae and Connaraceae, Matthews & Endress, 2002; Euphorbiaceae, Kapil, 1956; Linaceae, McDill et al., 2009). Heterostyly is present in two families of Oxalidales (Connaraceae, Lenza et al., 2008; Oxalidaceae, Luo et al., 2006) and in four families of Malpighiales (Clusiaceae, Lloyd & Webb, 1992; Linaceae, McDill et al., 2009; Erythroxylaceae, Del Carlo & Buzato, 2006; Turneraceae, Shore et al., 2006), and even tristyly occurs in both orders (Ganders, 1979). A tendency of the stamen bases to be united into a ring and nectaries located at the outer base of the stamens is present in all three orders (Matthews & Endress, 2005a). The presence of two ovules per carpel is common. Of particular interest is ovule structure. Predominantly they are incompletely tenuinucellar (or weakly crassinucellar) with an endothelium, while such ovules are largely lacking in other rosids (also present in some Brassicales) (for more details of their distribution, see Endress & Matthews, 2006b). Even if the ovules are crassinucellar, they are relatively narrow and often have an endothelium (Endress & Matthews, 2006b). Equally interesting is that the inner integument is mostly thicker than the outer (see also below). Ovules are mostly anatropous. Seeds with arils are relatively common (Endress & Matthews, 2006b). For a discussion of additional features, see Matthews and Endress (2005a).

CELASTRALES

Parnassiaceae are close to Celastraceae in floral morphology (Matthews & Endress, 2005a) and have been incorporated into them (APG, 2009). The third family, Lepidobotryaceae, is more distinct. Flowers are commonly small. In Lepidobotryaceae and many Celastraceae, they are functionally unisexual. Petals are not retarded in development and they become the protective organs in floral bud (Matthews & Endress, 2005a). Stamens form a single antesepalous whorl, but not in Lepidobotryaceae. There are predominantly three carpels. Stigmas are commissural, but not in Lepidobotryaceae. The ventral slit of the carpels is postgenitally connected by long, interlocking epidermal cells, and the pollen tube–transmitting tract is unusually conspicuous and encompasses several cell layers as seen in transverse section (Matthews & Endress, 2005a). Nectaries commonly form conspicuous discs.

OXALIDALES

The order consists of six families and is well supported. The flowers have predominantly isomerous whorls (thus more than three carpels). Sepal aestivation is commonly valvate, and the sepals are postgenitally connected (but quincuncial imbricate in Oxalidaceae and Connaraceae) (Matthews & Endress, 2002). Obdiplostemony is common. The pollen tube–transmitting tract is commonly restricted to a single cell layer around an open canal (Matthews & Endress, 2002). Placentation is always axile. Most commonly there are two or slightly more ovules per carpel. Ovules are commonly bitegmic and anatropous, but hemitropous or almost orthotropous ovules occur (however scarcely) in some Oxalidaceae, Connaraceae, Cunoniaceae, and Elaeocarpaceae (Matthews & Endress, 2002). The micropyle is commonly formed by both integuments (Matthews & Endress, 2002).

MALPIGHIALES

Malpighiales are the largest order of angiosperms in terms of families (36 in APG, 2009, 40 in Wurdack & Davis, 2009). The families are more or less well supported; however, the topology of families within the order is poorly resolved, except for a few small groups of families (Davis et al., 2005; Tokuoka & Tobe, 2006; Korotkova et al., 2009; Wurdack & Davis, 2009). Two of these subclades, Chrysobalanaceae s.l. with five families and Rhizophoraceae s.l. with ca. six families, were the first to be comparatively studied in floral structure (Merino Sutter & Endress, 2003; Matthews & Endress, 2008, in prep.). The realization of the position of the giant-flowered Rafflesiaceae within Malpighiales, close to the small-flowered Euphorbiaceae (Davis et al., 2007, 2008; Barkman et al., 2008; Davis, 2008), was surprising, and comparative studies on the floral structure will be necessary to understand the evolution of Rafflesiaceae.

Floral monosymmetry is present in at least 11 families (e.g., do Carmo E. Amaral, 1991; Matthews & Endress, 2008; Zhang et al., 2010). Glands on the outer sepal surface are known from several families. They are probably mainly nectaries, but in the South American Malpighiaceae they are oil glands essential in pollination biology (Vogel, 1974). Polystemony occurs in several families. It can be centrifugal or bidirectional, which, e.g., allows distinction of Salicaceae from Achariaceae, both former components of the defunct Flacourtiaceae (Bernhard & Endress, 1999). Synandry occurs in representatives of more than 10 families (Matthews & Endress, 2008). A trend to form stamen fascicles is present in several families (Fig. 7A–C) (Euphorbiaceae, Prenner et al., 2008; Clusiaceae, Leins & Erbar, 1991; Stevens, 2007; Sweeney, 2008; Hypericaceae, Leins, 1964; Rhizophoraceae, Breteler, 2008). Although incompletely tenuinucellar or weakly crassinucellar ovules with an endothelium are reported from at least 19 families, crassinucellar ovules without an endothelium also occur in at least 15 families. Antitropous ovules (Endress, 1994), usually combined with an obturator, are recorded from at least 17 families (e.g., Merino Sutter et al., 2006). A nucellar beak is common in the earlier Euphorbiaceae s.l., which are now distributed to several families (present in Euphorbiaceae and Phyllanthaceae, Sutter & Endress, 1995, and Picrodendraceae, Merino Sutter et al., 2006), as is vascularization of the integument(s) (present in taxa of Euphorbiaceae, Phyllanthaceae, Picrodendraceae, and Putranjivaceae; Merino Sutter et al., 2006). Arils appear to occur, especially in combination with crassinucellar ovules.

MALVIDS (EUROSIDS II)

Core malvids are made up of Brassicales, Malvales, Sapindales, and the recently recognized Huerteales (Worberg et al., 2009). Huerteales are very poorly known in terms of floral structure. The recent addition of Geraniales, Myrtales, Crossosomatales, and Picramniales (APG, 2009; H. C. Wang et al., 2009) is still not well supported molecularly. Nevertheless, malvids are easier to characterize in floral structure than fabids, even with the addition of the four noncore orders. Furthermore, mitochondrial DNA supports a relationship of the COM clade with malvids (Zhu et al., 2007; Qiu et al., in press), which was earlier suggested based on floral structure (Endress & Matthews, 2006b). However, this relationship was not found in Burleigh et al. (2009) and H. C. Wang et al. (2009).

In Picramniales, Sapindales, Huerteales, and many Brassicales, small flowers are predominant. Functionally unisexual flowers are also common. Multiple evolution of monosymmetric flowers (but commonly not very elaborate monosymmetry) occured in core malvids and again in Myrtales and Geraniales (Fig. 8A–L). Except for Fabales (not in malvids), which have elaborate monosymmetry, among rosids the trend to monosymmetry is restricted to malvids, including the newly extended malvids and some Malpighiales (Endress, 1992, in prep.; Zhang et al., 2010). Monosymmetry tends to be oblique (i.e., not in the median plane) in some Sapindales and Brassicales (Ronse De Craene & Haston, 2006), as well as in Malpighiales (Matthews & Endress, 2008). Contorted petal aestivation is relatively common in core malvids and in Geraniales, Myrtales, and Malpighiales (Endress & Matthews, 2006b). A trend to form polystemony is conspicuous, not only in core malvids, but also in Myrtales and Malpighiales (Fig. 7). In addition, polystemony with stamen fascicles is present in Malvales (Malvaceae, Nyffeler & Baum, 2001; von

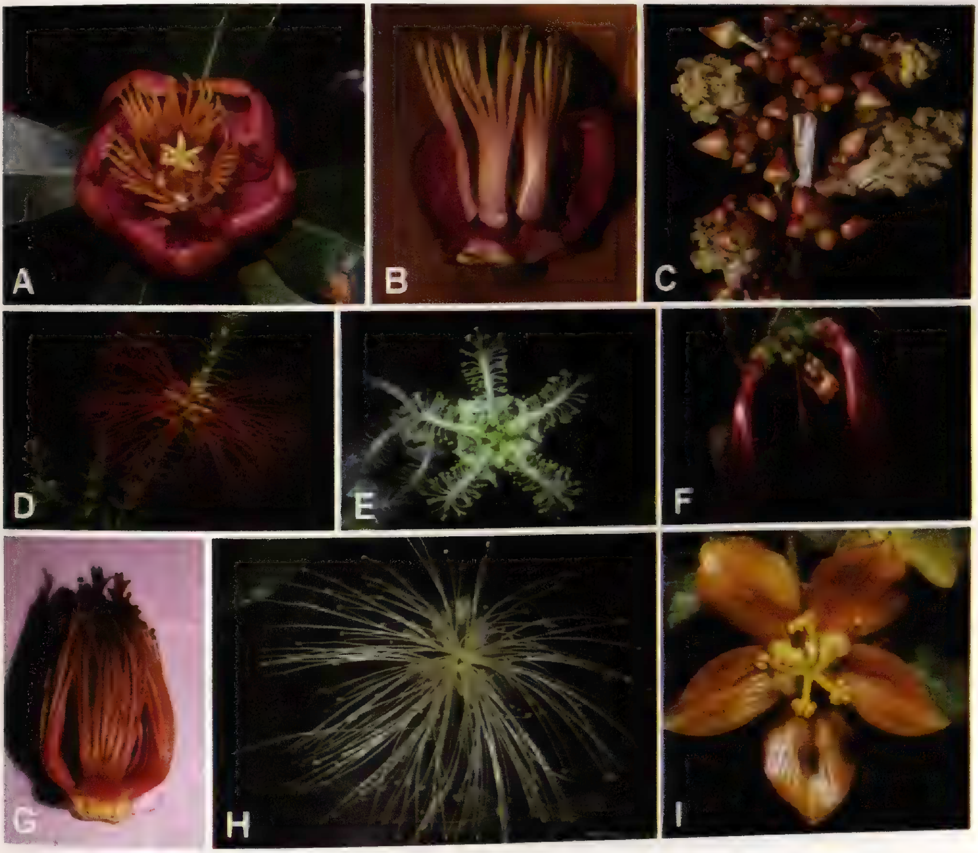

Figure 7. Malvids and potentially related groups. Stamen fascicles. A–C. Malpighiales. —A, B. Clusiaceae (*Montrouziera gabriellae* Baill.). —C. Euphorbiaceae (*Ricinus communis* L.). D–F. Myrtales. —D. Myrtaceae (*Beaufortia sparsa* R. Br.). —E. Myrtaceae (*Lophostemon confertus* (R. Br.) Peter G. Wilson & J. T. Waterh.) (photo by Rudolf Schmid). —F. Myrtaceae (*Calothamnus chrysantherus* F. Muell.). G–I. Malvales. —G. Malvaceae–Bombacoideae (*Bombax buonopozense* P. Beauv.). —H. Malvaceae–Bombacoideae (*Pachira aquatica* Aubl.). —I. Malvaceae–Bombacoideae (*Fremontodendron californicum* (Torr.) Coville).

Balthazar et al., 2004, 2006), Myrtales (Myrtaceae, Bohte & Drinnan, 2005), plus Malpighiales (see above). A gynophore or androgynophore (i.e., a stipe below the gynoecium or androecium) is preferentially found in core groups of the malvids (Fig. 8M–Q), but is also present in Crossosomatales. Gynoecia with three carpels are quite common, but there is also a trend to form gynoecia with more than five carpels in a whorl in core malvids (van Heel, 1995; Endress, 2006; Janka et al., 2008), and this is also represented in Myrtales and Malpighiales (Endress & Matthews, 2006b). In several core malvids (Malvales, Sapindales) plus Crossosomatales, the carpels are largely free, but as a compensation for the lacking internal compitum they become postgenitally fused at the tip, which allows the formation of a secondary compitum (Endress et al., 1983; Matthews & Endress, 2005b; Bachelier & Endress, 2008, 2009). Many groups of core malvids and some Geraniales, Myrtales, and Crossosomatales share campylotropous ovules with a zigzag micropyle (Endress & Matthews, 2006b). An especially interesting feature is the relative thickness of the two integuments of the ovules. In malvids and the COM clade, the inner integument is commonly thicker than the outer; in the other rosids it is the other way around, or both integuments are equally thick (Endress & Matthews, 2006b). The rare and striking Penaea type of embryo sac development (with four quartet modules, in the sense of Friedman & Williams, 2003) is, among angiosperms, only known from malvids, such as Sapindales (Biebersteiniaceae, Kamelina & Konnova, 1990) and Myrtales (Penaeaceae, Stephens, 1909), and from Malpighiales (Euphorbiaceae, Johri & Kapil, 1953; Malpighiaceae, Singh, 1961).

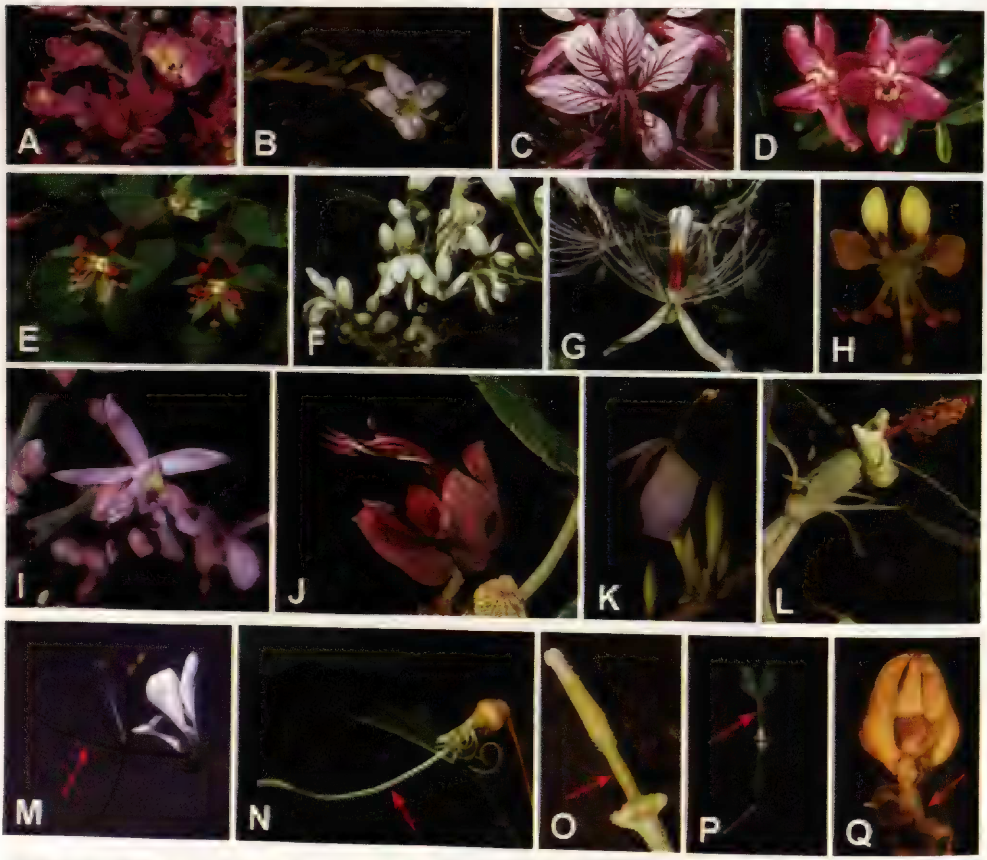

Figure 8. Malvids. A–L. Monosymmetric flowers in families of three orders. —A–D. Sapindales. —A. Sapindaceae (*Aesculus carnea* Zeyher). —B. Sapindaceae (*Cossinia pinnata* Comm. ex Lam.). —C. Rutaceae (*Dictamnus albus* L.). —D. Rutaceae (*Ravenia spectabilis* (Lindl.) Planch ex Griseb.). —E–H. Brassicales. —E. Tropaeolaceae (*Tropaeolum pentaphyllum* Lam.). —F. Moringaceae (*Moringa oleifera* Lam.). —G. Capparaceae (*Capparis micracantha* DC.). —H. Cleomaceae (*Cleome violacea* L.). —I–L. Malvales. —I. Malvaceae–Byttnerioideae (*Kleinhovia hospita* L.). —J. Malvaceae–Bombacoideae (*Chiranthodendron pentadactylon* Larreat). —K. Malvaceae–Helicteroideae (*Helicteres* sp.). —L. Malvaceae—Malvoideae (*Hibiscadelphus distans* L. E. Bishop & Herbst). M–Q. Flowers or young fruits with pronounced gynophores (arrows) in families of three orders. M–O. Brassicales. —M. Cleomaceae (*Cleome gynandra* L.). —N. Capparaceae (*Steriphoma paradoxum* Endl.). —O. Brassicaceae (*Lunaria rediviva* L.). —P. Sapindales: Rutaceae (*Boenninghausenia albiflora* (Hook.) Meisn.). —Q. Malvales: Malvacee (*Firmiana simplex* W. Wight).

GERANIALES

Geraniales consist of three to six families, of which Geraniaceae and Melianthaceae are the most prominent ones. Petals are commonly retarded in development up to anthesis. There are as many carpels as sepals (mostly five or four) (Ronse De Craene & Smets, 1999; Ronse De Craene et al., 2001). Ovules are crassinucellar and anatropous (Melianthaceae, Mauritzon, 1936; Ledocarpaceae, Boesewinkel, 1997) or campylotropous (mostly Geraniaceae, Boesewinkel & Been, 1979; Vivianiaceae, Boesewinkel, 1997). The two integuments tend to be equally thick (three cell layers each) (Boesewinkel & Been, 1979; Boesewinkel, 1988, 1997). Nectaries are on staminode-like organs (Melianthaceae: *Greyia* Hook. & Harv. and *Francoa* Cav.) or on the outer base of stamens (Geraniaceae) (Ronse De Craene et al., 2001).

MYRTALES

Myrtales comprise nine to 13 families, with Combretaceae basal (Sytsma et al., 2004). Sepals are valvate (in at least six families). Petals are sometimes extremely retarded in bud and have a narrow base. Often there is an extensive floral cup, with the result that the insertion areas of the narrow petals are far apart from each other (e.g., Schönenberger & Conti, 2003). Stamens tend to be incurved in bud (Dahlgren

& Thorne, 1984). Polystemony is common (Fig. 7D–F) and is based on centripetal stamen initiation (Mayr, 1969; Leins, 1988; Bohte & Drinnan, 2005; Kadereit, 2005; Leins & Erbar, 2008). Carpels are united up to the stigma; stigmatic lobes are commissural in Onagraceae (Mayr, 1969) and Penaeaceae (Rao & Dahlgren, 1968; Schönenberger & Conti, 2003). The ovary is mostly inferior, and, in addition, there is a neck (a long intercalated zone between the base of the outer floral organs and the inferior ovary) in some Combretaceae (Tiagi, 1969) and Onagraceae (Carlquist & Raven, 1966). Ovules are crassinucellar, often campylotropous, and the two integuments are regularly equally thick (two cell layers each) (e.g., Tobe & Raven, 1987, 1990, 1996).

CROSSOSOMATALES

Crossosomatales contain seven or eight families that were scattered in very different orders before it was recognized that they formed a clade (Nandi et al., 1998; Savolainen et al., 2000; Cameron, 2003; Sosa & Chase, 2003; Oh & Potter, 2006). In contrast to Geraniales and Myrtales, petals tend to be protective in bud (Matthews & Endress, 2005b). Sepals are imbricate, with the outer smaller than the inner. Flowers tend to have a floral cup. So-called pollen buds (intine protrusions at the apertures) are common (Matthews & Endress, 2005b; Oh & Potter, 2006). Gynoecia are apocarpous or syncarpous, but the carpels are initially free at least above the ovary (except Stachyuraceae), but most fuse postgenitally toward the tip, forming an extragynoecial compitum (Matthews & Endress, 2005b; Oh & Potter, 2006). The gynoecium or the free carpels may be shortly stalked (gynophore or stipe). Ovules are crassinucellar and tend to have relatively long integuments forming a zigzag micropyle. The outer integument is thicker than the inner (Matthews & Endress, 2005b). An aril is present in several families (Matthews & Endress, 2005b).

PICRAMNIALES

Picramniales are a new order (APG, 2009) based on a single family erected by Fernando and Quinn (1995). Detailed floral morphological studies are lacking. Flowers are minute and unisexual. Perianth and androecium comprise 3- to 5-merous whorls. The gynoecium is 2- or 3-carpellate, syncarpous, with two ovules per locule (Fernando & Quinn, 1995).

SAPINDALES

Sapindales consist of nine families, including a basal grade of Biebersteiniaceae and Nitrariaceae and a poorly resolved core clade (Muellner et al., 2007). Functionally unisexual flowers appear to be common (e.g., Harms, 1940; Renner et al., 2007; Bachelier & Endress, 2007, 2008, 2009), combined with heterodichogamy at least in Kirkiaceae and Sapindaceae. A trend toward floral monosymmetry is present (Fig. 8A–D). Petals tend to be the protective organs in floral buds and often have a valvate aestivation and incurved tips (Bachelier & Endress, 2009). The ovary is commonly superior. The presence of one or two ovules per carpel is predominant. Ovules are crassinucellar, relatively many are campylotropous, and in four families pachychalazal ovules occur (e.g., Corner, 1976). They are commonly bitegmic, but unitegmic ovules have been reported in at least four families of the core clade (Wiger, 1935; Boesewinkel & Bouman, 1978; Bachelier & Endress, 2009).

HUERTEALES

The flowers in this new order of three families are very poorly known apart from the original species descriptions (Worberg et al., 2009) (see also under Eurosids). Only female flowers of *Perrottetia* were described in more detail (Matthews & Endress, 2005a). Flowers are small and unisexual. A floral cup is common. There are one or two ovules per carpel.

BRASSICALES

Brassicales, the glucosinolate-producing order, at present contains 17 families (APG, 2009), eight or nine of which form the core Brassicales (Hall et al., 2004). A trend toward floral monosymmetry is present (Fig. 8E–H). Floral dimery associated with double organ positions in corolla and androecium, and sometimes increase in carpel number, are characteristic for a group of families in the core Brassicales (Endress, 2002; Ronse De Craene & Haston, 2006), whereas the basal state in the order is probably pentamery (Ronse De Craene, 2002; Ronse De Craene & Haston, 2006). Unisexual flowers regularly occur in several families (e.g., Hall et al., 2004). Sepals are the protective organs in floral bud and petals are often retarded in development (pers. obs.; Ronse De Craene & Haston, 2006). Gynophores, although present in several orders of malvids, are especially pronounced in Brassicales. The carpels are commonly united up to the top. Ovules are mostly crassinucellar without an endothelium (incompletely tenuinucellar or weakly crassinucellar and with an endothelium only in Brassicaceae, and weakly tenuinucellar without an endothelium in Koeberliniaceae, Limnanthaceae, and Tropaeolaceae). Relatively many groups have campylotropous ovules with a zigzag micropyle, especially in the core Brassicales, whereas basal families tend to have anatropous ovules (Tobe & Raven, 2008). The inner integument is thicker than the outer in most of the core Brassicales, whereas the reverse is the case in the basal groups. Limnanthaceae have only one integument (Maheshwari & Johri, 1956). Ovules with vascular bundles in the integument are present in several basal families but are absent in core Brassicales (Tobe & Raven, 2008). Arils occur scattered in at least six families.

MALVALES

Malvales currently embrace 10 families (APG, 2009). A trend toward floral monosymmetry is present, especially in Malvaceae (Fig. 8I–L). Polystemonous androecia with centrifugal stamen initiation on a ring meristem or on five sectorial primary primordia are common (Fig. 7G–I) (Malvaceae, van Heel, 1966; von Balthazar et al., 2004, 2006; Janka et al., 2008; Cistaceae, Nandi, 1998a). In Bombacoideae and Malvoideae of Malvales, the androecial units are monothecal (Endress & Stumpf, 1990; Bayer & Kubitzki, 2003) or rarely even without any thecal structure (von Balthazar & Nyffeler, 2002). Thus the malvalean androecium is a hot spot region of evolutionary events. For gynoecium structure, see the discussion under Malvids. Ovules are crassinucellar and the micropyle is formed by both integuments and often has a zigzag shape. However, in Cistaceae and Dipterocarpaceae (Nandi, 1998b) and Cytinaceae (Igersheim & Endress, 1998), ovule curvature is weak and they are orthrotropous or hemitropous. A nucellar beak is present in some Malvaceae and Thymelaeaceae. In the developing seeds, a bixoid chalaza is unique in Malvales and is represented in Cochlospermaceae, Bixaceae, Cistaceae, Dipterocarpaceae, and Sarcolaenaceae (Nandi, 1998b), which form a subclade in Malvales (Nickrent, 2007); it was found also in Sphaerosepalaceae and Thymelaeaceae (Horn, 2004). There is a vascular bundle in the outer integument in some Dipterocarpaceae (Rao, 1955) and Malvaceae (Rao, 1954). Nectaries are present in the form of carpets of multicellular hairs on the upper surface of the sepals or adjacent areas in many Malvaceae, (Vogel, 2000) or in the form of discs in Cytinaceae, Muntingiaceae, and Sarcolaenaceae (Vogel, 2000; Horn, 2004), but are lacking altogether in Bixaceae and most Cistaceae and Dipterocarpaceae, which produce only pollen as a reward (Vogel, 2000). Apodanthaceae (earlier Rafflesiales) are a parasitic family with uncertain position (APG, 2009), fluctuating between Malvales (Nickrent, 2002) and Cucurbitales (Barkman et al., 2007). Apodanthaceae share three almost unique characters with Malvales but nothing of comparable distinction with Cucurbitales: the androecium has an athecal organization and forms a congenitally uniform tube around the style, and a carpet of unicellular to multicellular hairs is present on the inner base of the perianth organs (Blarer et al., 2004). Thus structural features support a position in Malvales.

ASTERID LINEAGE S.L.

The asterid lineage s.l. has a basal grade of five orders and two major large clades, the lamiids and campanulids. Although the composition of the orders is well supported, the exact position of Berberidopsidales, Santalales, and Caryophyllales is still not clear, and therefore they are not included in asterids s. str. (APG, 2009). All eudicots with a free central placenta bearing more than one ovule are in this clade (perhaps except for Podostemaceae). In the ovules there is a tendency toward a thin nucellus. Crassinucellar ovules are rare in the asterid lineage s.l. (only in Caryophyllales crassinucellar ovules are common, in addition to weakly crassinucellar ovules). More common are weakly crassinucellar, incompletely tenuinucellar, tenuinucellar, and reduced tenuinucellar ovules. It is of special interest that this is also true for Santalales and Caryophyllales with their unsettled position. The ovules are unitegmic, except for some basal clades (bitegmic in most Caryophyllales, a few Santalales, many Ericales, and two unplaced families in lamiids: Vahliaceae and perhaps Icacinaceae, see below). If there are two integuments, the micropyle is consistently formed by the inner one (Berberidopsidales, Mauritzon, 1936; van Heel, 1977; Kubitzki, 2007; Santalales, Fagerlind, 1948; Caryophyllales, Eckardt, 1976; Ericales, e.g., Tsou, 1994; Vahliaceae, Raghavan & Srinivasan, 1942).

BERBERIDOPSIDALES

Of the two families in Berberidopsidales, the floral structure of Aextoxicaceae (Kubitzki, 2007; Ronse De Craene & Stuppy, 2010) appears quite different from that of Berberidopsidaceae (van Heel, 1977; Ronse De Craene, 2004). The enigmatic genus *Streptothamnus*, a possible additional member of the order, is insufficiently known (Ronse De Craene, 2004). Berberidopsidales are therefore difficult to characterize at this point.

SANTALALES

Santalales are an order of mainly parasitic plants in seven families (Malécot & Nickrent, 2008; APG, 2009). The flowers are in general small and inconspicuous, except for some bird-pollinated Loranthaceae. Petal aestivation is consistently valvate. Nectaries, if present, are lobes or rings around the gynoecium. There are various trends of reduction in floral organization. In the first trend the perianth is affected. The sepals, still equal in size to the petals in some Olacaceae (Endress, 2008), become small and disappear, and the petals have both protective and attractive functions. In the extreme case (female flowers of Balanophoraceae), the entire perianth disappears (Endress, 1994; Wanntorp & Ronse De Craene, 2009). In the second trend the gynoecium is affected. At first the ovary septa, then the integuments, then the ovules (Fagerlind, 1948), and finally the entire inner morphological space of the gynoecium gradually disappear (*Balanophora* J. R. Forst. & G. Forst., Fagerlind, 1945b). Only some Olacaceae still have two integuments (Fagerlind, 1948). The other groups are unitegmic (Santalaceae p.p., Bhatnagar & Sabharwal, 1969; Olacaceae p.p., Fagerlind, 1947), ategmic (Misodendraceae, Skottsberg, 1913; Santalaceae p.p., Ram, 1959a, b), or lack ovules (some Loranthaceae, Johri & Bhatnagar, 1961). The ovules with a nucellus still present are reduced tenuinucellar (Fagerlind, 1947; Bhatnagar & Sabharwal, 1969) or incompletely tenuinucellar (Ram, 1957). Chalazal endosperm haustoria occur in all families (in Loranthaceae already the embryo sacs behave like haustoria); in some families micropylar haustoria also occur (Skottsberg, 1913; Maheshwari et al., 1957; Swamy, 1960; Agarwal, 1961; Bhatnagar & Sabharwal, 1969). Molecular phylogenetic studies recently showed that Balanophoraceae are part of Santalales (Nickrent et al., 2005). However, this systematic position has long been quite clear from the unique reduction of the gynoecium and the uniquely bent embryo sac. In Santalaceae, the reduction of the inner part of the ovary results in sharp bending of the embryo sac as it grows from the short ovule into the placenta. In *Balanophora*, although the inner morphological surface has completely disappeared and thus the embryo sac and the embryo develop in the compact gynoecium because no ovule and seed are formed, this sharp bend is retained (figures in Johri & Bhatnagar, 1961). This is an example of an unusual evolutionary trend and a unique structural feature for prediction of relationships between *Balanophora* and Santalales. Further support is provided by the male flowers, which have a valvate perianth and synandria as in some Santalaceae (Endress & Stumpf, 1990; Eberwein et al., 2009).

CARYOPHYLLALES

Caryophyllales in the current circumscription consist of two major subclades: (1) the classical Caryophyllales s. str. (Centrospermae) and (2) a newly circumscribed subclade added later (Albert et al., 1992). Two families of the latter, Polygonaceae and Plumbaginaceae, were also sometimes positioned close to Caryophyllales earlier. Caryophyllales s. str. are well characterized by floral structure (Eckardt, 1976; Hofmann, 1994), especially their uniform and unique ovule structure (campylotropous, with both integuments often only two cell layers thick, micropyle formed by the thickened rim of the inner integument, air space between the outer and inner integument at the base, nucellar cap, perisperm) (Rocén, 1927; Eckardt, 1976), whereas the second subclade has fewer conspicuously shared floral features and the ovules are anatropous (campylotropous in Frankeniaceae, Walia & Kapil, 1965). However, in both subclades there is a trend to form dimerous or trimerous gynoecia with late closing ovaries and a single basal ovule (Amaranthaceae, Hakki, 1972; Basellaceae, Sattler & Lacroix, 1988; Caryophyllaceae, Hofmann, 1994; Nyctaginaceae, Rohweder & Huber, 1974; Phytolaccaceae, Eckardt, 1955; Plumbaginaceae, De Laet et al., 1995; Polygonaceae, De Laet et al., 1995). Ovules commonly have long funicles (Amaranthaceae, Ronse de Craene et al., 1999; Cactaceae, Leins & Schwitalla, 1985; Caryophyllaceae, Rohweder, 1970; Nyctaginaceae, Rohweder & Huber, 1974; Plumbaginaceae, De Laet et al., 1995; Polygonaceae, Solntseva, 1983), equally thick integuments, and the micropyle formed by the inner integument, which has a thickened rim. The second subclade tends to have contorted petal aestivation.

As Santalales, Caryophyllales are also characterized by a simple perianth in many families, but in contrast, the petals are lacking (and not the sepals). This is the case in Simmondsiaceae, Physenaceae (Dickison & Miller, 1993), Achatocarpaceae, Amaranthaceae, Gisekiaceae, Phytolaccaceae, Sarcobataceae, Nyctaginaceae, Halophytaceae, Cactaceae, Portulacaceae, some Caryophyllaceae, and, in the second clade, Nepenthaceae and Polygonaceae. Apetaly is most likely basal in Caryophyllales and petals have arisen more than once in the order (Brockington et al., 2009). In some families, the colored perianth organs appear to correspond to sepals and not petals (Cactaceae, Nyctaginaceae, Phytolaccaceae, Portulacaceae) (Rohweder & Huber, 1974). In the derived Aizoaceae, Portulacaceae, and Cactaceae, sepal, stamen, and carpel numbers tend to be increased. Stamens (and in derived Aizoaceae the strongly androecium-related petals) are initiated centrifugally from ring meristems (Leins et al., 2001). Nectaries, if present, are commonly ring-shaped areas, often at the inner androecium base, but are not distinctly disc shaped.

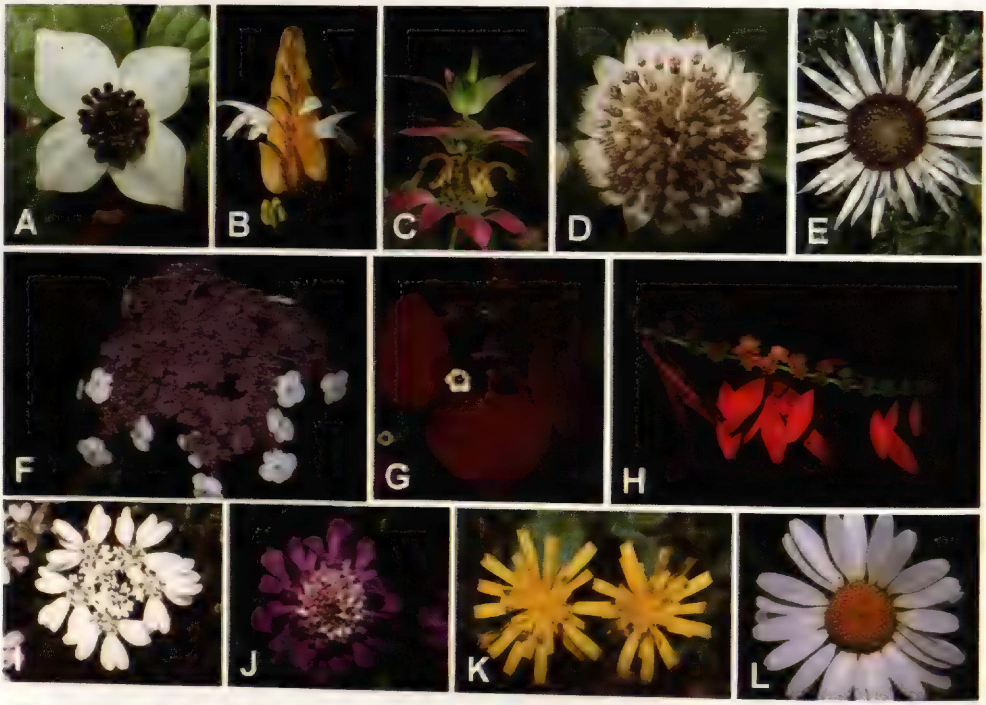

Figure 9. Asterids. Pseudanthia with radiating colored peripheral organs of three different kinds and with different systematic distribution. A–E. Colored bracts (across all major subclades of asterids). —A. Cornaceae (*Cornus canadensis* L.). —B. Acanthaceae (*Pachystachys lutea* Nees). —C. Lamiaceae (*Monarda punctata* L.). —D. Apiaceae (*Astrantia major* L.). —E. Asteraceae (*Carlina acaulis* L.). F–H. Colored sepals (especially in Cornales and Rubiaceae of Gentianales). —F. Hydrangeaceae (*Hydrangea aspera* Buch.-Ham. ex D. Don). —G. Rubiaceae (*Mussaenda erythrophylla* Schumach. & Thonn.). —H. Rubiaceae (*Warszewiczia coccinea* Klotzsch). I–L. Colored and differentially enlarged petals (especially in campanulids). —I. Apiaceae (*Orlaya grandiflora* (L.) Hoffm.). —J. Caprifoliaceae (*Scabiosa lucida* Vill.). —K. Asteraceae–Cichorioideae (*Hieracium murorum* L.). —L. Asteraceae–Asteroideae (*Leucanthemum vulgare* Lam.).

ASTERIDS

Asterids show predominant sympetaly, and also a higher occurrence of synsepaly than rosids. However, synsepaly is unstable and often varies at the family or genus level. Unitegmic, incompletely tenuinucellar ovules with an endothelium are predominant. Endosperm haustoria are widespread.

Flowers exhibit high synorganization of floral organs, with peaks in (1) Gentianales (Apocynaceae with fusions between almost all organs and pollen transport with translators), (2) Lamiales (highly specialized lip flowers in several families), and (3) Asterales (Asteraceae and relatives with postgenitally fused anthers and elaborate pollen release).

As a consequence of high organ synorganization, in some groups there is secondary pollen presentation, with at least three main occurrences: in some Ericales (especially epacrid Ericaceae, e.g., McConchie et al., 1986), in Gentianales (Loganiaceae, Erbar & Leins, 1999, and Rubiaceae, Igersheim, 1993; Puff et al., 1996, and in a very unusual way by pollinia attached to translators in Apocynaceae, M. E. Endress, 2001), and in Asterales (Asteraceae, Campanulaceae, Calyceraceae, Goodeniaceae) (Leins & Erbar, 2006).

In addition to the floral organs in the flowers being highly integrated in various ways, the flowers in the inflorescences are often integrated in forming pseudanthia as they are best known in Asteraceae. Three morphological patterns of pseudanthia may be distinguished, which also have different characteristic systematic distributions (Fig. 9). The first pattern (Fig. 9A–E) has colored bracts and is scattered over the entire asterids, even in some Asteraceae (e.g., *Carlina* L. and *Helichrysum* Mill.) (Schnell, 1960; Napp-Zinn & Heins, 1979; Classen-Bockhoff, 1990; Funk et al., 2009). The second pattern (Fig. 9F–H) has increased sepals, either at the periphery of the inflorescence or everywhere (Weber, 1955; Schnell, 1960; Classen-Bockhoff, 1990, 1996); it occurs in some Hydrangeaceae of Cornales and some Rubiacae of Gentianales. The third pattern (Fig. 9I–L) is the most integrated, with increased petals in flowers at the periphery of the inflorescence; the petals may be differentially increased, i.e., the more peripheral they are, the larger they are. This pattern especially occurs in campanulids; it is the familiar situation in Asteraceae, but is also represented in Apiales (e.g., *Orlaya* Hoffm., *Heracleum* L.) and Dipsacales (e.g., *Scabiosa* L., *Viburnum* L.).

It is noteworthy that the most species-rich clades of asterids, Lamiales, Gentianales, and Asteraceae, have elaborate (except for Gentianales, which are mostly monosymmetric) flowers with practically uniformly two carpels. They also have the most extremely tenuinucellar ovules. Other asterids often have three carpels, more rarely five or even more, and more often incompletely tenuinucellar ovules. In a number of clades, the ovules are completely unvascularized, which need more comparative study.

GRADE OF BASAL ASTERIDS

The first two orders in asterids, Cornales and Ericales, which form a grade, have retained two whorls of stamens in several families, a trait that is otherwise extremely rare in asterids, known only in *Dialypetalanthus* Kuhlm. (Rubiaceae) and Paracryphiaceae. More often than in core asterids (euasterids) there are flowers with more than five sepals and petals in Cornales and Ericales (and also in some Gentianales and Apiales). There is also a trend to form polyandrous flowers in some clades of both orders. Flowers are polysymmetric with very few exceptions and never elaborately monosymmetric. Gynoecia predominantly have more than two carpels, mostly three to five.

CORNALES

Cornales have relatively simple flowers (except for Loasaceae), with the sepals often reduced, the petals both protective and attractive, and valvate, and the stamens in one or two whorls. However, polystemonous flowers are present in most Hydrangeaceae (Hufford, 1998, 2001) and Loasaceae (Hufford, 1990, 2003), and in Hydrangeaceae with centripetal and centrifugal initiation patterns (Hufford, 2001; Ge et al., 2007). Inferior ovaries are common. Ovules are never tenuinucellar, but mostly incompletely tenuinucellar, weakly crassinucellar, or even crassinucellar (the latter in some Cornaceae [Kamelina & Shevchenko, 1988] and some Nyssaceae [Tandon & Herr, 1971]).

ERICALES

Ericales comprise 22 or more families (Schönenberger et al., 2005; APG, 2009), some of which form more or less well-supported subclades (numeration as in Schönenberger et al., 2005: 276: I, Marcgraviaceae–Tetrameristaceae–Balsaminaceae; II, Polemoniaceae–Fouquieriaceae; III, the families of the former Primulales plus Ebenaceae plus Sapotaceae; IV, Diapensiaceae–Styracaceae–Symplocaceae; Va, Ericaceae–Cyrillaceae–Clethraceae; Vb, Sarraceniaceae–Actinidiaceae–Roridulaceae).

The flowers in Ericales are unusually diverse, and those of some subclades appear far apart from others at first sight but share structural patterns in detail (Schönenberger & Grenhagen, 2005; Schönenberger, 2009; Schönenberger et al., 2010). An extreme case is the basal subclade I of Marcgraviaceae–Tetrameristaceae–Balsaminaceae: The unusually elaborate monosymmetric flowers of Balsaminaceae appear to be the result of a rapid and recent diversification and anagenesis (Janssens et al., 2009). However, floral synapomorphies with the related Marcgraviaceae and Tetrameristaceae are still present (Schönenberger et al., 2010). A trend to form polystemonous flowers is present in more than one subclade (Actinidiaceae, van Heel, 1987; Lecythidaceae, Tsou & Mori, 2007; Theaceae, Tsou, 1998). Subclade V p.p. has anthers that are inverted at anthesis and have porelike slits (Stevens et al., 2004). In subclade Vb, nectar is not produced (except for some Sarraceniaceae) and the flowers offer only pollen to pollinators (Schmid, 1978; Renner, 1989). Double positions of stamens (see Floral Phyllotaxis) occur in Fouquieriaceae (Schönenberger & Grenhagen, 2005) and were also found in the Cretaceous ericalean fossil *Paradinandra* (Schönenberger & Friis, 2001). In subclade III, antepetalous stamens and a free central placenta are highly characteristic, and nectaries, if present, are unusual; a (small) disc around the ovary base is only known from *Coris* L. (Myrsinaceae). Otherwise, nectaries are either inconspicuous areas of the upper ovary wall (in the basal family Maesaceae and some Primulaceae) or form patches of secretory hairs (Theophrastaceae and some Myrsinaceae) (Vogel, 1997). Ericales have retained another primitive trait in some families: ovules with two integuments. In these ovules there is, in turn, another interesting pattern: in some families the inner integument is thicker than the outer, and in others it is the other way around. The first is the case in the families of subclade III but not Sapotaceae (e.g., Warming, 1913; Dahlgren, 1916; Subramanyam & Narayana, 1968; Rao, 1972). In the diverse family Balsaminaceae, transitional steps between bitegmic and unitegmic ovules are present (McAbee et al., 2005). The second is the case in more basal families of Ericales (e.g., Tsou, 1994; McAbee et al., 2005). Ovules are often campylotropous and in most groups are incompletely tenuinucellar with endothelium; however, in many Lecythidaceae (Tsou, 1994), Myrsinaceae (Dahlgren, 1916), Sapotaceae (*Mimusops* L.) (Bhatnagar & Gupta, 1970), and Pentaphylacaceae (Ternstroemiaceae) (Tsou, 1995), an endothelium is lacking. In subclade Va and in Primulaceae and Diapensiaceae, the ovules are tenuinucellar, in the latter without endothelium (Samuelsson, 1913; Vijayaraghavan, 1969). In at least seven families, but not in subclade Va, the outer or only integument is vascularized; only in some Theaceae the base of the inner integument is vascularized (e.g., Warming, 1913; Bhatnagar & Gupta, 1970; Tsou, 1994, 1997). Endosperm haustoria are mainly present in subclade Va but are absent in a number of other families (Judd & Kron, 1993). Ericalean flowers are unusually well represented in the fossil record of the Cretaceous, which indicates an early rich diversification in the order (Christophel & Basinger, 1982; Friis, 1985; Nixon & Crepet, 1993; Keller et al., 1996; Schönenberger & Friis, 2001; Crepet et al., 2004; Schönenberger, 2005; Friis et al., 2006a; Crepet, 2008; Martínez-Millán et al., 2009).

EUASTERIDS

Euasterids contain two large clades, lamiids and asterids, both conspicuously diversified at various levels and with some very species-rich subclades, such as the order Lamiales and the families Rubiaceae (Gentianales) and Asteraceae (Asterales). Especially conspicuous is the trend to form elaborate monosymmetric flowers in the Lamiales–Solanales clade and, in a different way, in Asterales (Asteraceae, Campanulaceae), always combined with oligandry (Endress, 1990; Jabbour et al., 2008).

LAMIIDS (EUASTERIDS I)

The basal split of lamiids separates Garryales from the core lamiids, the latter being made up of three clades of unresolved topology, Lamiales–Solanales, Gentianales, and Boraginales (APG, 2009). Lamiids are in general characterized by late sympetaly, in which the petals are free from each other at initiation and become confluent later, as discussed by Erbar (1991) and Erbar and Leins (1996). However, this feature is probably a mere consequence of a superior ovary, which is present in most lamiids (see discussion on campanulids). This is supported by those few lamiid families with an inferior ovary, which, as expected, have early sympetaly, such as Aucubaceae (Reidt & Leins, 1994), Rubiaceae (Erbar & Leins, 1996), and Sphenocleaceae (Erbar, 1995). Contorted petal aestivation is present in many lamiids with polysymmetric flowers, whereas cochlear aestivation is common in monosymmetric flowers. An almost exclusive character of lamiids is a pollen sac placentoid (i.e., a parenchymatic longitudinal ridge protruding into each pollen sac from the center of the anther), as found by Hartl (1963). It is overwhelmingly present in Lamiales and is also found in many Solanales. In Gentianales, in some Gentianaceae a tapetal (and not parenchymatic) pollen sac placentoid is present; the same occurs in *Ixorhea* Fenzl (Boraginales, Di Fulvio, 1978). Outside of lamiids, weakly differentiated tapetal pollen sac placentoids may be present in Escalloniaceae (*Escallonia* Mutis ex L. f., Kamelina, 1984) and Apiaceae (*Phlojodicarpus* Turcz. ex Ledeb., Grevtsova, 1987), as seen from illustrations. The presence of numerous ovules on protruding diffuse placentae is common in all orders (except Garryales) but not ubiquitous in any of them. Vascular bundles in the ovule integument are largely absent (except for some Oleaceae and Convolvulaceae). Petaloid sepals, explosive flower opening, and buzz pollination, although not characteristic for lamiids as a whole, have sparsely evolved in several subgroups, whereas they appear to be lacking in campanulids.

GARRYALES

The flowers of the small order Garryales are unisexual, simple, and more or less reduced. Two of the three families (Garryaceae and Eucommiaceae) are wind pollinated and lack petals and nectaries. Eucommiaceae also lack sepals. Ovaries are inferior (not applicable for *Eucommia* Oliv. because of its lack of outer floral organs). Garryales have unusual ovules: they are crassinucellar (not just weakly crassinucellar) and the micropyle is curved in an anticampylotropous direction (curvature in the opposite direction of a normal campylotropous ovule; Aucubaceae, Satô, 1971; Alimova & Shinkina, 1987; Eucommiaceae, Eckardt, 1963; Sogo & Tobe, 2006; Garryaceae, Kapil & Rao, 1966). Crassinucellar ovules are otherwise not common in asterids, but also occur here and there in other, mostly smaller, groups, such as some Cornales, Aquifoliales, and Solanales, and anticampylotropous curvature is also rare otherwise.

LAMIALES AND SOLANALES

There is a conspicuous trend to form monosymmetric flowers, sometimes very elaborate ones, especially in Lamiales (Fig. 10) (Reeves & Olmstead, 2003). Monosymmetry is especially expressed in the corolla, commonly also in the androecium by

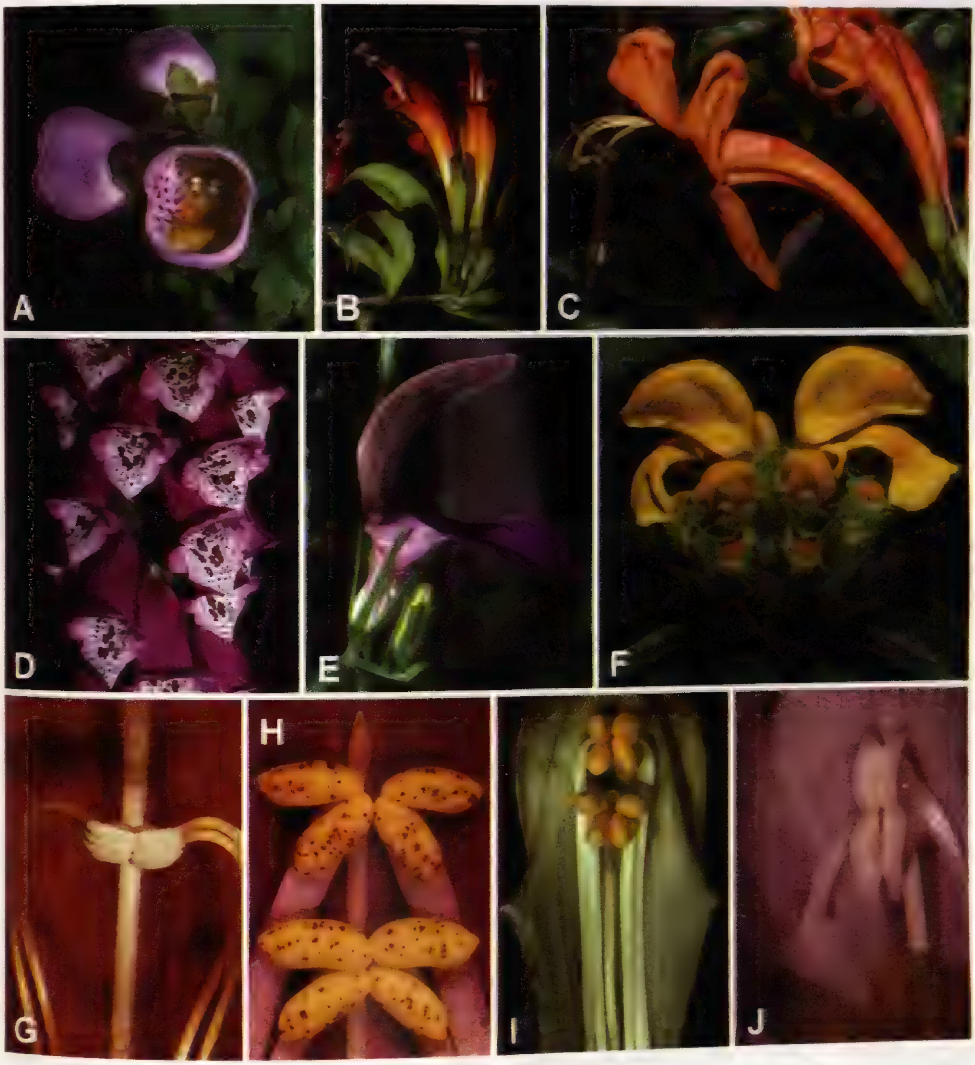

Figure 10. Lamiales. Monosymmetric flowers. A–F. Entire flowers. —A. Calceolariaceae (*Jovellana violacea* G. Don). —B. Gesneriaceae (*Aeschynanthus speciosus* Hook.). —C. Bignoniaceae (*Tecomaria capensis* (Thunb.) Spach). —D. Plantaginaceae (*Digitalis purpurea* L.). —E. Acanthaceae (*Brillantaisia nitens* Lindau). —F. Lamiaceae (*Phlomis fruticosa* L.). G–J. Pollination organs: median orientation of style and anthers. —G. Gesneriaceae (*Columnea* sp., the four anthers postgenitally united). —H. Plantaginaceae (*Digitalis purpurea* L., the anthers of each of the two pairs contiguous by converging turgescent filaments). —I. Plantaginaceae (*Antirrhinum majus* L., the anthers of each of the two pairs contiguous by parallelly oriented turgescent filaments. —J. Linderniaceae (*Torenia fournieri* E. Fourn., only one stamen pair present, the two anthers contiguous by converging turgescent filaments).

reduction of the upper (median) stamen and much more rarely in one of the stamen pairs. Because the stamens are aligned pairwise in the symmetry plane, flanking the style and stigma (Fig. 10G–J), presence of a well-formed median stamen could easily obstruct the functioning of the pollination apparatus or not allow herkogamy, which may explain the predominant reduction of the median stamen. This trend occurs in a large portion of Lamiales and in Solanaceae. It is commonly associated with cochlear petal aestivation (i.e., imbricate with one organ completely outside and one inside).

LAMIALES

Lamiales are one of the large orders in lamiids, with several of its families richly diversified. Phylogenetic studies have led to profound changes in the circumscription and arrangement of the families (Wagstaff & Olmstead, 1998; Olmstead et al., 2001; Tank et al., 2006).

Although pentamerous flowers are most common, in basal families tetramerous flowers appear to be predominant (Oleaceae, Sehr & Weber, 2009; Tetrachondraceae, Wagstaff, 2004; Calceolariaceae, Endress, 1999; Mayr & Weber, 2006). Floral monosymmetry (of pentamerous flowers) is especially predominant and in many groups there are very elaborate bilabiate flowers, with an upper and lower lip and the pollination organs more or less sheltered in the concave upper lip (Fig. 10) (Endress, 1994; Weber, 2004; Westerkamp & Classen-Bockhoff, 2007). The extent of the reduction of the median stamen (as mentioned above) varies; sometimes it is not even initiated. The degree of reduction appears to be more or less correlated with the degree of expression of monosymmetry, and it is also often more or less constant even in larger subclades (Endress, 1998, 1999). For instance, the median stamen is completely lacking in Lamiaceae, Acanthaceae, and Orobanchaceae, but it is consistently present at least as a staminode in Gesneriaceae and Bignoniaceae (Endress, 2001a). In some cases, one of the stamen pairs is also reduced, so that only two functional stamens are left. This occurs in parallel in some genera of several families: Acanthaceae, Lamiaceae, Scrophulariaceae, and Plantaginaceae. A trend to form synthecal anthers (with the two thecae confluent over the apex) is exhibited in Gesneriaceae, Lamiaceae, Plantaginaceae, and Scrophulariaceae (Endress & Stumpf, 1990). In certain cases, the presence or lack of a median stamen has indicated that a genus was wrongly placed. The enigmatic *Rehmannia* Libosch. ex Fisch. & C. A. Mey. and *Paulownia* Siebold & Zucc. completely lack a median stamen (Endress, 1998; Fischer, 2004), which does not support a position in Gesneriaceae or Bignoniaceae, respectively, as earlier assumed, but both come out close to Orobanchaceae in molecular studies (Tank et al., 2006; Albach et al., 2009; Xia et al., 2009), which is supported by the lack of a staminode. The gynoecium is constantly bicarpellate (with extremely rare exceptions, such as in *Duranta* L., Verbenaceae, Bocquillon, 1863), but there is a tendency for reduction to pseudomonomery in several families (Acanthaceae, Schönenberger & Endress, 1998; Phrymaceae, Eckardt, 1937; Verbenaceae, Bocquillon, 1863; Plantaginaceae, Eckardt, 1937). Ovules are predominantly tenuinucellar and also often incompletely tenuinucellar and have an endothelium; they are anatropous or campylotropous. Prominent micropylar and chalazal endosperm haustoria are characteristic. The water plant family Hydrostachyaceae, positioned for some time in Cornales, now appears to be close to the base of Lamiales (Burleigh et al., 2009), which is supported by the presence of tenuinucellar ovules (Rauh & Jäger-Zürn, 1966) and endosperm haustoria (Jäger-Zürn, 1965), neither present in Cornales (see also Leins & Erbar, 1988).

SOLANALES

Flowers of Solanales are commonly polysymmetric, but several monosymmetric genera also occur in both larger families of the order, Solanaceae and Convolvulaceae, and even some cryptic asymmetry by different levels of anther exposition is present in both families (Endress, in prep.). There is a trend to form funnelform or rotate flowers with only very short free petal parts (many Convolvulaceae and Solanaceae). A few genera of Solanaceae have a similar kind of floral monosymmetry and reduction of the odd stamen as do Lamiales (Robyns, 1931; Huber, 1980; Hunziker, 2001; Ampornpan & Armstrong, 2002), or the odd stamen and one of the stamen pairs (several genera, Hunziker, 2001), whereas in the rare monosymmetric flowers in Convolvulaceae, all five stamens are well developed (*Humbertia* Lam., *Ipomoea lobata* (Cerv.) Thell.) (Deroin, 1992).

GENTIANALES

Gentianales comprise two major subclades: the large family Rubiaceae plus a cluster of families including Gentianaceae, Apocynaceae, Gelsemiaceae, and Loganiaceae, of which Apocynaceae are also large (Backlund et al., 2000). Apocynaceae are another group with complex flowers, but complex in a very different direction than Lamiales. They are polysymmetric, not monosymmetric. Floral organs are exceedingly synorganized with each other and form organ complexes (Schick, 1982; Fallen, 1986; Endress, 1994; Endress & Bruyns, 2000; M. E. Endress, 2001). In general, in Gentianales petals are often contorted, but there is also a trend from contorted to valvate aestivation. In both Apocynaceae and Rubiaceae, there are groups with the corolla postgenitally united above the basal congenitally united (sympetalous) zone and there sometimes fenestrate (Fallen, 1986; Robbrecht, 1988; Endress, 1994; Endress & Bruyns, 2000). Among asterids, pollen dispersal, not in monads but in higher aggregations (tetrads, pollinia), is mainly concentrated in Gentianales (some Apocynaceae, Gentianaceae, Rubiaceae). So-called pollen buds (intine protrusions at the apertures) are also an unusual feature of scattered occurrence in some Gentianales (Apocynaceae, Huang, 1986; Gentianaceae, Drexler & Hakki, 1979; Rubiaceae, Weber &

Igersheim, 1994). Carpels that are flat (not plicate) and postgenitally united in the style or in some cases even in the ovary occur in some Apocynaceae (Fallen, 1985), Gentianaceae (Kissling et al., 2009), and Rubiaceae (Puff et al., 1996; De Block & Igersheim, 2001). The ovules show several unusual features. They are tenuinucellar (not incompletely tenuinucellar)—in some groups even reduced tenuinucellar—but an endothelium is lacking and endosperm haustoria are absent or poorly developed. Some groups that were erroneously placed in Gentianales, but have been recognized as members of other orders by molecular studies, had been excluded from Gentianales earlier because of their ovules, such as Menyanthaceae (earlier in Gentianaceae), which are incompletely tenuinucellar and have an endothelium and a vascularized, thick integument (Stolt, 1921; Inoue & Tobe, 1999). They are now in Asterales, and *Polypremum* L. (earlier in Loganiaceae), which has an endothelium and a haustorial endosperm (Moore, 1948), is now in Tetrachondraceae of Lamiales.

BORAGINALES

Polysymmetric, funnel-shaped or rotate flowers with only short free petal parts are common in different subgroups of the single family Boraginaceae (if the former Hydrophyllaceae, Cordiaceae, Ehretiaceae, and Lennoaceae are all lumped into Boraginaceae, APG, 2009). Boraginales show a trend to an increase of floral merism, either in the perianth and androecium, as in *Codon* L. (in basal position, Ferguson, 1999) and *Cordia* L., or in the gynoecium of the parasitic *Lennoa* Lex. and *Pholisma* Nutt. ex Hook. (Yatskievych & Mason, 1986). Ovules, although often incompletely tenuinucellar (Berg, 2009), tend to be weakly crassinucellar in more than one subclade (*Cordia*, Khaleel, 1982; *Ehretia* P. Browne, Johri & Vasil, 1956; *Heliotropium* L., Khaleel, 1978), and endosperm haustoria are only chalazal (Billings, 1901; Berg, 2009) or inconspicuous (Johri & Vasil, 1956; Khaleel, 1978).

UNPLACED GROUPS IN LAMIIDS

The unplaced families in lamiids—Vahliaceae, Icacinaceae, Metteniusaceae, and Oncothecaceae (APG, 2009)—are poorly known in floral structure and embryology. *Vahlia* Thunb. has bitegmic ovules with the micropyle formed by the inner integument (Raghavan & Srinivasan, 1942), and rudimentary bitegmy was also reported from *Phytocrene* Wall. (Icacinaceae) (Fagerlind, 1945a). *Metteniusa* H. Karst. (González & Rudall, 2010) shares long, valvate petals and a unilocular ovary with two pendant ovules with Icacinaceae. So far no conspicuous floral structural features have come up that would suggest specific relationships of these families with any of the larger subclades.

CAMPANULIDS (EUASTERIDS II)

As lamiids, campanulids also show a basal split with a small order (Aquifoliales) and an unresolved complex of three (partly) larger clades (core campanulids). The core campanulids comprise Escalloniales, Asterales, and a clade of Bruniales, Apiales, and Dipsacales plus Paracryphiales (APG, 2009).

In addition to the pattern of pseudanthia with enlarged peripheral petals of the peripheral flowers mentioned before (Fig. 9I–L), campanulids are characterized by early sympetaly, in which the corolla appears to be initiated as a ring primordium on which secondarily the petals become apparent (Erbar & Leins, 1996). This is probably a consequence of another characteristic of the campanulids, the dominance of inferior ovaries (see also Endress, 1997a; Roels, 1998). In such flowers, the floral apex becomes more or less concave in early floral development, long before the time of gynoecium initiation, which may then give the impression of a ring primordium when the corolla is initiated. Ronse De Craene and Smets (2000) discuss the difference between early and late with regard to the position of stamen primordia: either on the rim or inside the rim of the early cavity. Petals are commonly valvate with incurved tips and somewhat postgenitally united in bud (in addition to the congenitally united base) and thus have a protective function, whereas the calyx is modified into a pappus or a group of bristles or thorns in various groups of Asterales (Asteraceae, Calyceraceae, *Brunonia* Sm. ex R. Br. of Goodeniaceae) and Dipsacales (Dipsacaceae). In contrast to lamiids, contorted petal aestivation is largely absent. In Apiales and Asterales, petals sometimes have three or more vascular traces. Presence of a single ovule per carpel or gynoecium is common though not ubiquitous. Integumentary vascular bundles are common in Asterales and Dipsacales (Billings, 1901; Kamelina, 1980). Elaborations related to buzz pollination are almost absent (present only in some Pittosporaceae).

AQUIFOLIALES

The flowers are commonly small. Sepals are short, and petals are protective organs in bud, most commonly with a valvate aestivation and a conspicuously inflexed tip. Carpels have two (or one) pendant ovules. Crassinucellar ovules turned up in three of the four families studied so far: Aquifoliaceae (Herr, 1959), Cardiopteridaceae (Fagerlind, 1945a), and Stemonuraceae (Padmanabhan, 1961); in Aquifoliaceae, curiously, these ovules have a well-developed endothelium.

ESCALLONIALES

The two families Escalloniaceae and Polyosmaceae have flowers with a tube formed by the basal part of the petals, which tend to be valvate and more or less postgenitally connected. The gynoecium has a long, completely united style and an inferior ovary with more or less parietal placentae. Except for a species of *Escallonia* (Kamelina, 1984), the ovules are unstudied.

ASTERALES

Asteraceae, the most species-rich family of Asterales (and of all angiosperms), have attained the ability to produce both polysymmetric and monosymmetric flowers in the same inflorescences, especially in the largest subfamily, Asteroideae (Kim et al., 2008; Funk et al., 2009). Although this versatility is also present here and there in other campanulids, it became a key innovation in Asteraceae. A striking theme in Asterales is secondary pollen presentation from the upper part of the style based on pronounced protandry. The style, to which the open anthers are appressed (in some subclades by postgenital fusion of the anthers), carries the pollen upward by elongation at the male stage, and pollination occurs by transport from there to flowers at the female stage (Erbar & Leins, 1995; Leins & Erbar, 2006). This is ubiquitous in the largest family, Asteraceae, but is also present in Calyceraceae, Goodeniaceae, and Campanulaceae. In Stylidiaceae, androecium and gynoecium are congenitally fused so that pollen presentation on the upper part of the style is primary and not secondary. It is noteworthy that the families without secondary pollen presentation are all species-poor (Alseuosmiaceae, Argophyllaceae, Menyanthaceae, Pentaphragmataceae, Phellinaceae, Rousseaceae). Petals with two conspicuous wings, associated with induplicate-valvate aestivation, are shared by three families of the Pacific clade of Lundberg (2009) (Alseuosmiaceae, Goodeniaceae, and Menyanthaceae). In at least three families of Asterales (Asteraceae, Harling, 1950; Campanulaceae, Rosén, 1932; Goodeniaceae, Rosén, 1946), genera with more than two meiocytes in the nucellus occur. Tenuinucellar ovules are predominant in Asteraceae and also occur in Pentaphragmataceae and Stylidiaceae, whereas incompletely tenuinucellar ovules are present in the other families studied. An endothelium is most common. The subclade of four families including Asteraceae (Lundberg, 2009) is characterized by ovules with a thick (more than 10 cell layers) and vascularized integument, not only Goodeniaceae and Asteraceae as mentioned by Tobe and Morin (1996), but also Calyceraceae (Dahlgren, 1915) and Menyanthaceae (Stolt, 1921; Inoue & Tobe, 1999); this character is present in parallel in Campanulaceae (Campanuloideae, but not Lobelioideae) (Kamelina & Shinkina, 1998) from another subclade of Asterales. Endosperm haustoria are common, but were not found in some families.

BRUNIALES

The assemblage of Bruniaceae, Columelliaceae, and Desfontainiaceae as order Bruniales (APG, 2009, based on Winkworth et al., 2008) needs profound comparative research in its floral structures. Shared characters of all three families are slight floral monosymmetry and a superior ovary (both not in all Bruniaceae). However, the close mutual relationship of these families is not obvious from what is known on their flowers to date.

APIALES

Flowers are commonly small. The calyx is often reduced to a small rim. The corolla is protective in bud. The incurved tip of the valvate petals is conspicuous in some Araliaceae (Nuraliev et al., 2010) and in Apiaceae (lobulum inflexum) and attains a diversity of forms (Jahnke & Froebe, 1984). A conspicuous trend to form polystemonous androecia (based on a single whorl of stamens) and, to a lesser degree, multicarpellate gynoecia, is present in Araliaceae (Endress, 2002, 2006; Sokoloff et al., 2007a). Commonly, there is only one ovule per carpel or even per gynoecium (Karehed, 2003). The occurrence of crassinucellar ovules in Aralidiaceae (Philipson & Stone, 1980) and some Araliaceae (D. Singh, 1954) and of weakly crassinucellar ovules in Griseliniaceae (Alimova, 1987) and some other Araliaceae is noteworthy. Nevertheless, the most common type is incompletely tenuinucellar, usually with an endothelium (lacking in Pittosporaceae). Campylotropous ovules are common. Some of the small families are poorly known in their floral structure (Pennantiaceae, Torricelliaceae, Melanophyllaceae).

DIPSACALES

Flowers are predominantly monosymmetric in Caprifoliaceae, which represent the majority of genera in the order, but polysymmetric in Adoxaceae;

monosymmetry in Caprifoliaceae may be based on duplications in *DipsCYC* genes (Howarth & Donoghue, 2005). Subtle asymmetries are caused by fertility of only one of the more than two carpels or formation of only one lateral stamen (Hofmann & Göttmann, 1990; Endress, 1999; Donoghue et al., 2003). The corolla is protective in bud (Roels & Smets, 1996). Floral nectar is secreted by dense carpets of multicellular hairs on the corolla base in both Adoxaceae and Caprifoliaceae, a character not known from other asterids (Wagenitz & Laing, 1984). Carpels (or often entire gynoecia) are consistently uniovulate. Ovules are weakly crassinucellar in *Viburnum* (Adoxaceae) (Suneson, 1933) and otherwise incompletely tenuinucellar.

PARACRYPHIALES

In Paracryphiaceae and Sphenostemonaceae, there is an unusually low level of synorganization of floral parts. Sepals are caducous and petals are lacking; there is a trend of increase in stamen number up to more than 10 (Gilg & Schlechter, 1923; Jérémie, 2008). In Paracryphiaceae, the number of carpels is also increased, up to 15 (Endress, 2002; Jérémie, 2008). In both families, the gynoecium is barrel-shaped with a superior ovary and sessile stigma. Another unusual feature in Paracryphiaceae is that the stamens tend to be arranged in two whorls, as seen from their alternation with the sepals (Dickison & Baas, 1977: fig. 10). This low synorganization appears to be the reason why the representatives of the two families were originally placed in basal angiosperms (Paracryphiaceae in Chloranthaceae, and Sphenostemonaceae in Monimiaceae or Trimeniaceae). In contrast, Quintiniaceae have 4- or 5-merous flowers with sepals and petals, and a style and inferior ovary of three to five carpels (Engler, 1930). Paracryphiaceae and Quintiniaceae may have crassinucellar ovules, and in Quintiniaceae ovules may even be bitegmic (Dickison & Baas, 1977; Mauritzon, 1933: fig. 43B). Superficial floral structural features do not support a close relationship of Quintiniaceae with the other two families. Comparative studies on the floral structure and development of the three families are badly needed.

Conclusions and Outlook

Among the features explored in this study, there are some that have not been conventionally considered in the characterization of larger clades (from the top of the phylogenetic hierarchy downward). (1) Structural features of the sporophytic domain of ovules are strongly underexplored and are a promising field of study at higher systematic levels. It appears that some features of ovule diversity are even more strongly correlated with larger clades than previously assumed (e.g., integument number and thickness; nucellar differentation at the apex, flanks, and base at early meiosis; degree and direction of ovule curvature at anthesis; presence or absence of endothelium). With regard to other ovular domains, formation of endosperm haustoria and structure of the embryo suspensor may be promising to explore further at the morphological level (traditionally only the cellular level has been considered, e.g., cellular vs. nuclear endosperm or cellular division patterns in the proembryo, Albach et al., 2001). (2) Distinction between congenital and postgenital fusion in and between carpels has often been neglected but is needed for a better functional and systematic understanding of the gynoecium. With regard to intercarpellary fusions, a specific gynoecial architecture is well represented in malvids. In several subclades, carpels are initially free in development, at least in their upper part, but later fuse postgenitally, which allows formation of a functional compitum in a different way from the common case in syncarpous gynoecia (Crossosomatales, Sapindales p.p., Malvaceae p.p.) (Endress et al., 1983; Matthews & Endress, 2005b; Bachelier & Endress, 2008, 2009). The feature is also known in more isolated occurrence from Sabiaceae (Endress & Igersheim, 1999), Iteaceae of Saxifragales (Hermsen et al., 2003), and some Gentianales (Endress et al., 1983). (3) The relationships between sepal and petal development in flowers also have not been comparatively studied previously. It has been recognized in the present study that petals more often than earlier believed (e.g., by Endress, 1994) are not retarded in development but overtake the sepals and become protective organs, beginning at a relatively early stage and often attaining a valvate aestivation. Such early-developing protective petals also tend to have broad (not narrow) bases. Several clades show a trend toward this behavior (e.g., Vitales, Gerrath & Posluszny, 1989; Celastrales, Matthews & Endress, 2005a; Crossosomatales, Matthews & Endress, 2005b; Sapindales, Bachelier & Endress, 2009; Santalales, Wanntorp & Ronse De Craene, 2009; Cornales, Hufford, 2001; campanulids, e.g., Gustafsson & Bremer, 1995). This adds a new facet to the old and persistent problem of sepal and petal identity and needs to be explored in additional clades and in more developmental detail.

Similar trends of specialization occur in many larger clades. When mapped on a cladogram of angiosperms, some features appear as potential key innovations in more than one clade (e.g., compitum, Fig. 1, feature 3) in rosids and asterids, tricolporate pollen (feature 4) in rosids (minus Saxifragales) and asterids, incompletely tenuinucellar ovules (feature 5) in the COM clade and asterids (minus Cornales), elaborate monosymmetric flowers (feature 9) in Fabales of the nitrogen-fixing clade, in core lamiids, and in core campanulids. It is of interest to explore to what extent these features having evolved many times across eudicots or across subclades of eudicots are based on the same genetic machinery and, vice versa, how different they may be (e.g., Cronk, 2002). It appears that genetic systems for specific features are present in certain plant groups even if these features are not manifested there. An example is the genetic structure responsible for floral monosymmetry in large groups of core eudicots, which was present much earlier in eudicot evolution than in those large groups with monosymmetric flowers in which it was initially detected (Cubas et al., 2001; Howarth & Donoghue, 2006). Thus, those clades in which particular features appear for the first time, especially novel features that are regarded as key innovations, were explored here. The first occurrence of such features is often much earlier than when they appear at the base of a large clade where they may be regarded as key innovations (Endress, 2001b) (e.g., on Fig. 1, 5-merous flowers, compitum, tricolporate pollen, haplostemony, tenuinucellar ovules). However, not all innovations became key innovations. Such delay in the establishment of a feature as a key innovation was discussed in detail at the generic level in spur evolution of *Halenia* Borkh. in an ecological and phylogeographic context (Kadereit & von Hagen, 2003). From the present study, the phenomenon seems also widespread at higher systematic levels (and thus over larger time spans). In these, in addition to ecological factors, morphological factors may also play a role in that the global floral architecture may not yet be predisposed for a key innovation, even though a critical feature was already manifested (cf. Fig. 1). An interesting example of the present study is floral monosymmetry. In malvids, although there is a conspicuous trend to monosymmetric flowers, monosymmetry is never very elaborate and has not been a key innovation in this clade. In contrast, in Lamiales, monosymmetry is more elaborate and has been a key innovation leading to great diversification.

Another long-known phenomenon apparent in this study is that each clade has different regions in the flowers that are evolutionarily active or unstable as hot spots for evolution and likewise regions that are inactive as cold spots for evolution. For instance, Ranunculaceae are hot or dynamically variable in carpel number, while Rosaceae are seen to vary for carpel number and fusion. Santalales reveal diverse forms in carpel reduction, while Leguminosae vary in stamen number and floral symmetry. In marked contrast, carpel number is a cold spot in lamiids and campanulids, where carpels are almost invariably two. A detailed demonstration and discussion of such hot and cold evolutionary spots move beyond the scope of this paper and should be the topic of a separate work.

In cases of uncertainty in the position of clades, floral features may provide support. This is briefly discussed for several clades, such as (1) COM clade as closer to malvids than fabids, (2) Apodanthaceae, with a position in Malvales rather than Cucurbitales, (3) Balanophoraceae, as in Santalales, (4) Hydrostachyaceae, associated with Lamiales rather than Cornales, (5) *Rehmannia*, evinced as closer to Orobanchaceae rather than Gesneriaceae or Scrophulariaceae, and (6) *Paulownia*, as affined closer to Orobanchaceae rather than Bignoniaceae or Scrophulariaceae.

In summary, it should be emphasized again that newly recognized clades need to be comparatively studied in structural features. This is an ongoing necessity. Likewise, unconventional floral features need to be explored, i.e., features that have not been previously considered by morphologists, embryologists, and systematists in their conventional catalog of features for comparative studies. Another exciting challenge will be to further explore in what aspects the features of parallel trends of specialization are similar and in what aspects they differ, including in a molecular developmental genetic context.

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